SOIL FAUNA OF MEDITERRANEAN-CLIMATE REGIONS

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INTRODUCTION

The two most distinctive features of mediterranean-climate ecosystems are probably the dominance of sclerophyllous plants in the above-ground subsystem and the life at depth of numerous groups of hygrophilous animals in the soil subsystem. For most of these groups, life in the deep soil habitat must be considered as an **escape** response (Di Castri, 1973c), or a mechanism of **avoidance** (Wallwork, 1976), related to the fluctuations of the mediterranean climate, particularly the summer drought, and perhaps the high frequency of fire.

At a geological scale, paleoclimatic phases of glaciation and desiccation progressively impelled hygrophilous arthropods with poor capacity for active or passive dispersal to migrate in depth searching for more stable microclimatic conditions. Some of them acquired peculiar **endogeous** adaptations, such as apterism and anophthalmy, body depigmentation, a cylindrical or filiform body associated with strong reduction of size, morphological structures to facilitate burrowing habits (cephalo-diggers and leg-diggers), and ultra-evolution of the male *aedeagus* in some soil beetles (Sáiz, 1973).

The present-day mediterranean environment, unlike for instance that of tropical or temperate rain forests, **requires** these hygrophilous groups to live at depth. On the other hand, this mediterranean environment (unlike that of tundras because of the permafrost layer, and that of some tropical savannas or temperate moorlands because of seasonal phenomena of flooding or waterlogging) also **allows** life at depth under aerobic conditions. Deep soils, some of them originated during more humid climatic periods, exist in mediterranean regions. In addition, the deep roots of mediterranean shrubs and trees provide input of organic matter to the low soil horizons, and the bedrock is generally in a strongly fractured form, thus favoring the penetration of soil animals. Finally, conditions of anoxia due to water saturation of the soil interstices are very rare in most of the mediterranean soils, because of the rolling topography of the areas and also of the occurrence of rainfall in the cold season (less oxidation processes).

It is true that strictly endogeous and hygrophilous animals (eu–edaphic elements) do not exist only in mediterranean soils, but also in all other ecosystems, particularly in the deciduous forest, where there are important seasonal fluctuations of temperature and/or precipitation while waterlogging does not occur. Furthermore, other ecological tolerances can be observed in soil-related animals of mediterranean areas, from more mesophilous groups (psocids, some pseudoscorpions and Prostigmata mites) up to very xerophilous ones, such as the tenebrionid beetles, the solifugids and the Caeculidae mites (Coineau, 1974). The response to the very high spatial and temporal heterogeneity of the mediterranean environment, which is increased even further by the innumerable soil microhabitats, is the multiplicity of mechanisms of survival and adaptation shown by the different groups and species of soil animals. Some of them will be illustrated in this chapter.

As regards the origin of these taxa, if most of the present-day mediterranean flora existed prior to the appearance of the mediterranean climate (Axelrod, 1973; Raven, 1973), this statement is valid *a fortiori* for most of the groups of mediterranean soil animals (Di Castri, 1973c). In fact, soil is a more stable and buffered environment than the above-

ground subsystem. The climatic seasonal fluc-
tuations are filtered, to a certain extent, by the
vegetation and the upper layers of litter and humus
(Di Castri, 1973a). Therefore, a constellation of
groups of the most diversified geological and
biogeographical origin, some of them so old as to be
considered living fossils, have been preserved in
mediterranean soils.

STATE OF KNOWLEDGE ON MEDITERRANEAN SOIL SUBSYSTEMS

The soils of mediterranean-climate regions, con-
sidered from a physico-chemical and morphological
point of view, or as regards their agricultural
potentiality, are reasonably well known (see also the
regional chapters in this volume). However, the soil
classifications adopted in the different mediter-
ranean regions and countries are often based on
national and local terms, thus making very hazar-
dous any attempt of intercontinental comparison.

It is hoped that the soil map of the world in
nineteen sheets at a scale 1:5 000 000, recently
completed by FAO–UNESCO (1970–1978), could
help to facilitate international comparability of soil
types. Just as one adds the Latin botanical term to a
vernacular plant name, it should be highly desirable
to follow the practice of giving the FAO–UNESCO
equivalent on first mention of a local soil name
(Young, 1979).

In addition, considering the heterogeneity of the
mediterranean landscape, it would be advisable to
study systematically the mediterranean soils along
environmental transects, and in terms of *catena*
(Zinke, 1973 or bioclimatic sequence, rather than
to attempt to define zonal soils. Multivariate
numerical methods of classification can be used to
characterize these soil sequences (Bottner et al.,
1975).

As regards soil biology and ecology in general,
the major problems facing ecologists in the study of
soil ecosystems have been outlined by Di Castri
(1970). Methodological aspects have been compre-
hensively reviewed by Phillipson (1971) for soil
ecology, and by Parkinson et al. (1971) specifically
for soil micro-organisms. The methods for extrac-
tion and sampling of soil animals have been dis-
cussed by Cancela da Fonseca and Vannier (1969)
and Vannier (1970) for arthropods, by Merny and

Luc (1969) for nematodes, by Bouché (1969) for
earthworms, and by Levieux (1969) for ants.

A preliminary synthesis on soil animal com-
munities in mediterranean-climate ecosystems has
been attempted by Di Castri (1973b). He described
in particular the physiognomy, stratification and
species diversity of soil communities; he also dis-
cussed the main selective forces acting on soil
organisms in the mediterranean environment, and
the evolutionary strategies adopted by soil animals
in response to these forces and on account of their
differing biogeographical origin. The world-wide
overview of Wallwork (1976) on the distribution
and diversity of soil fauna does not cover the
mediterranean ecosystems as such; however, some
consideration of mediterranean-climate soil ani-
mals is given in the chapters dealing with forests and
deserts.

In analyzing these preliminary syntheses, it must
be kept in mind that studies of soil as an ecological
system are relatively very recent, and that, above all,
the complexity of the soil subsystem as regards
number of species, of individuals and of micro-
habitats is several orders of magnitude greater than
that of the above-ground subsystem. Aquatic ani-
mals (the soil "water" fauna comprising small
animals, such as protozoans, rotifers and nem-
atodes, which dwell in the water-filled soil capil-
laries and the water film which envelops the soil
particles — see Kühnelt, 1955) live beside terrestrial
aerobic animals in a multiplicity of microhabitats
determined by small discontinuous variations in the
soil texture and by the stratification of soil into
horizons with very distinct conditions as living
spaces. For this environment, from a physical and
evolutionary viewpoint intermediate between the
atmosphere, the hydrosphere and the lithosphere.
Vannier (1973) proposed the denomination of *poro-
sphere*. This environment would have facilitated
the transition of invertebrates from the aquatic to
the terrestrial life (Ghilarov, 1958).

Three main problems appear when studying, and
even more when trying to compare, these soil
communities:

(1) The difficulties in taxonomic identification of
the organisms under study. To take the example of
Chile where the authors have worked during ten
years together with many collaborators, hundreds
of thousands of animals have been collected, and
hundreds of new species and many new genera have

been described, yet the taxonomy of most of the soil groups in Chile still remains largely unknown. The only practical solution is to concentrate research on a few selected groups — such as some mites, springtails (Collembola), pseudoscorpions, psocids and beetles — widely represented in these mediterranean environments.

(2) The lack of comparability of the extraction methods for the evaluation of density of soil animals adopted by different research workers in the various regions. For the purposes of this chapter, the core data consist of the materials collected by Di Castri and his collaborators, using strictly comparable techniques, in the mediterranean-climate zone of Chile (and to a lesser extent of the Mediterranean Basin and California). Whenever possible, comparisons will be made with the other mediterranean-climate regions.

(3) The lack of relations between the investigations on community structure of soil animals (density, species diversity, etc.) and those on functional aspects of the soil subsystem (litter fall and decomposition, soil biological activity attributable to metabolic processes of the microflora and to root respiration, etc.)[1]. For instance, though research on ecosystem functioning is well developed in California (Dunn and DeBano, 1977; Yeilding, 1977), "there is almost total absence of published information on soil animal communities in California" (Menke and Villaseñor, 1977). Conversely, in Chile the results of comprehensive research on soil animals are not backed by adequate information on chemical and biological aspects of soil metabolism.

STRUCTURE OF ANIMAL COMMUNITIES IN MEDITERRANEAN SOILS

The analysis of the structure of soil animal communities in mediterranean-climate regions will be based on the soil arthropods, which are often called soil mesofauna (Van der Drift, 1951; Balogh, 1958; Di Castri, 1963a) and measure from 0.2–0.5 up to 2–3 mm. In fact, they represent the large majority of the animals collected through the most commonly used extraction method, the Berlese–Tullgren funnels. A shorter mention will also be made of some aspects related to the small soil "water" animals (soil microfauna) and to the

soil macrofauna and megafauna (animals such as millipedes, termites, earthworms and others, whose dimensions go from less than 1 cm up to 20 cm or more). Some relationships of the soil fauna with the soil microflora, the ground-surface fauna (*epigaion* or epigeal fauna) and the plants will also be discussed.

Density and diversity of soil arthropods in mediterranean Chile

Data on density and diversity of soil arthropods in the mediterranean-climate region of Chile are summarized in Table 24.1 and Fig. 24.1. Only the commonest groups extracted by Berlese–Tullgren funnels are considered here. Mean density is expressed in number of individuals per dm^3 of soil; species diversity, in bits per individual according to the Shannon–Wiener function (Margalef, 1957). This method of measuring species diversity, based on information theory, was applied for the first time to problems of soil ecology by Di Castri et al. (1964) and Marcuzzi (1964), and it is widely used at present. The various ways in which this method has been applied to soil ecology, as well as the interpretation of the results obtained through it, are reviewed by Di Castri and Astudillo (1966a) and Cancela da Fonseca (1969). The two indices most commonly applied — that is, those of Shannon and of Brillouin — have been compared by Di Castri and Vitali-di Castri (1971).

Out of the thirteen ecosystem types considered in Table 24.1 and Fig. 24.1, eight represent "natural" conditions, though some of them have suffered a rather strong human impact; the last five are man-made systems resulting from the plantation of exotic trees, intensive agriculture, and irrigation. All of them are under xerothermomediterranean climatic conditions (mediterranean arid and semi-arid types, see Di Castri, Chapter 1) and are distributed from latitude 30 to 34°S.

The vegetation of this region is described in general terms by Rundel (Chapter 10). More information on ecosystem gradients in the central zone of Chile (semi-arid mediterranean type) can be found in Schlegel (1966), Quintanilla (1977), Armesto and Gutierrez (1978) and Armesto and

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[1] Information on soil biological activity of Mediterranean *garrigues* is available in Billés et al. (1975) and Cortez et al. (1975).

TABLE 24.1

Mean density (in individuals per dm³ of soil) of the main soil arthropod groups, extracted by means of Berlese–Tullgren funnels, from natural and man-modified ecosystems of the mediterranean-climate zone of Chile

| Main ecosystem types	Fog hygro-philous forest	Riparian hygro-philous forest	Deciduous forest	Sclero-phyllous forest	Sclero-phyllous matorral	*Acacia–Prosopis* savanna	Montane matorral	Open shrub-land with suc-culents	*Eucalyp-tus globulus* planta-tion	*Pinus radiata* planta-tion	Dry-farming fields	Irriga-ted crops	Irriga-ted pastures
Mean species diversity in bits per individual	4.49	4.11	4.28	3.97	3.74	3.39	3.43	3.30	2.82	2.33	3.17	2.95	2.56
Isopoda	9.3	49.0	2.1	12.5	3.8	5.5	0.9			0.4		2.6	8.0
Acarina													
Gamasides	185.3	152.6	198.7	94.1	43.2	69.7	3.0	6.1	62.1	9.3	14.7	14.9	402.6
Uropodina	108.7	31.4	57.1	22.7	4.7	9.1	0.5	0.1	9.7		2.0		1.0
Prostigmata	65.3	236.8	245.9	293.2	345.9	108.4	297.0	105.1	156.5	61.8	130.7	13.8	221.3
Tarsonemini	91.3	59.0	75.7	150.9	51.8	22.9	1.5	2.6	58.7	9.3	79.3	27.2	7.9
Acaridiae	50.0	369.3	115.1	73.8	25.8	65.6	16.5	18.4	55.2	16.4	57.3	269.8	2761.1
Oribatei	1633.3	1161.3	785.5	432.9	332.5	171.6	47.5	66.8	727.8	131.6	50.0	17.7	330.4
Araneida	6.7	3.7	11.3	6.5	4.6	2.2	0.6	0.8	1.9	0.9	0.1	0.5	3.5
Pseudoscorpionida	10.2	33.6	15.5	13.9	8.0	0.6	0.3	0.4	0.3				
Diplopoda	25.3	4.7	1.9	5.4	2.5	0.9	0.2	0.1	0.4			0.1	1.2
Pauropoda	8.7	2.0	0.4	2.2	0.8	0.1	0.5	0.2	0.4	0.9		0.9	3.0
Symphyla	0.9	1.0	1.2	2.8	0.3	0.6		0.1				0.4	0.5
Chilopoda	1.8	1.3	3.9	1.3	0.7	1.0	0.1	0.1	0.6			0.1	1.6
Collembola													
Arthropleona	146.0	354.3	115.9	184.4	39.5	105.8	54.7	18.5	392.9	19.6	4.7	89.6	3020.3
Symphypleona	2.5	28.3	1.6	5.6	0.6	6.5		0.8	6.9	4.4		4.3	3.8
Protura	16.0	5.7	5.8	4.7	3.8	0.2		0.2	1.3	0.4		2.2	0.9
Diplura	0.1		0.1	0.8	0.3	0.1		1.2				0.1	0.5
Thysanura			0.2	0.1	0.3	0.5		0.7					1.0
Thysanoptera	0.6	8.0	27.2	4.5	7.8	1.9	0.5	12.4	3.3		20.7	0.9	3.3
Psocoptera	0.8	1.3	5.7	9.1	17.9	1.5	0.5	3.6	2.7	1.3	0.9	0.3	15.0
Heteroptera	1.5	0.7	4.1	0.2	0.1	0.2	0.1	0.4	0.1		0.2	0.1	1.8
Homoptera	17.3	7.7	4.9	38.8	16.6	4.0	5.5	3.3	9.9		2.7	2.6	28.0
Lepidoptera (*larvae*)	16.7	4.7	11.7	3.7	3.8	1.3	0.6	0.8	4.7	0.9	0.7	3.3	5.7
Diptera (*larvae*)	8.0	10.7	36.2	18.0	5.9	69.5	6.5	3.8	9.7	0.4		4.7	20.2
Coleoptera (*larvae*)	5.3	8.0	20.3	5.3	2.2	3.7	0.5	3.5	0.4		0.2	0.9	9.0
Coleoptera (*imago*)	26.7	7.7	27.6	8.6	6.7	1.2	1.0	0.8	0.9		0.1	1.3	3.2
Hymenoptera	1.3	1.0	6.3	0.8	0.7	1.6	0.6	1.1			0.8	0.5	1.0
Total mean density (individuals per dm³ of soil)	2439.6	2543.8	1781.9	1396.8	930.8	656.2	439.1	251.9	1506.4	257.6	365.1	458.8	6855.8
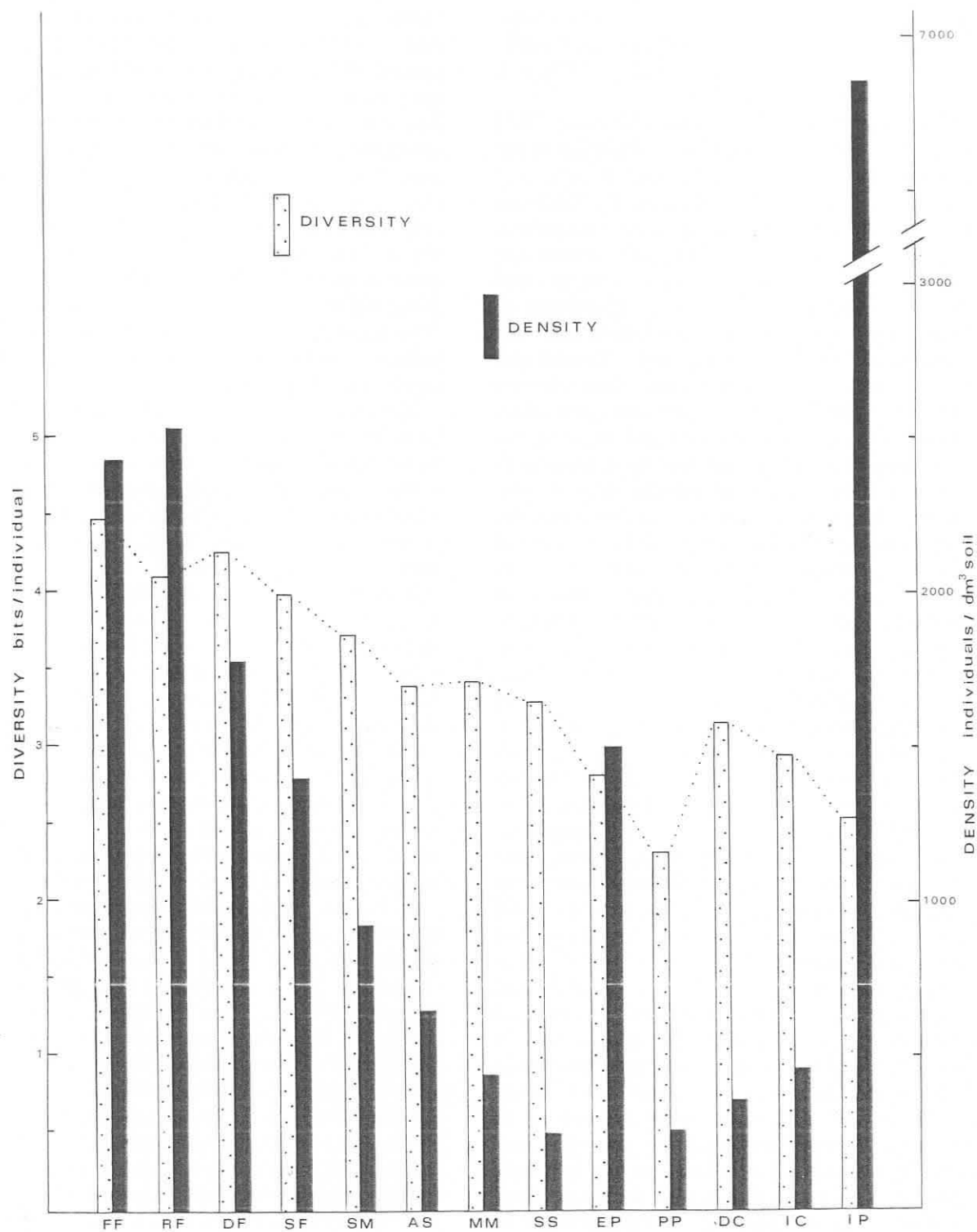
Fig. 24.1. Mean species diversity (in bits per individual, calculated according to Shannon's formula) and mean density (in individuals per dm³ of soil) of soil arthropods from thirteen natural and man-modified ecosystem types in the mediterranean-climate zone of Chile: *FF* = fog forest; *RF* = riparian forest; *DF* = deciduous forest; *SF* = sclerophyllous forest; *SM* = sclerophyllous matorral; *AS* = *Acacia* savanna; *MM* = montane matorral; *SS* = shrubland with succulents; *EP* = *Eucalyptus globulus* plantation; *PP* = *Pinus radiata* plantation; *DC* = dry-land cultivation; *IC* = irrigated crops; *IP* = irrigated pastures.

Martínez (1978); information related to the northern zone of Chile called *Norte Chico* (arid mediterranean type) is available in Bahre (1979) and Gastó and Contreras (1979).

The "fog" hygrophilous forests (*FF* in Fig. 24.1) occur with a very discontinuous distribution in the coastal range, and include several floristic and faunistic elements which characterize the Valdivian hygrophilous forests located about 800 km south of this mediterranean area; dominant species are *Aextoxicon punctatum*, *Drimys winteri* and *Beilschmiedia miersii*, with a great abundance of cryptogamic epiphytes and bromeliads (see also Kummerow, 1962; Follmann, 1963; Rundel and Weisser, 1975). The riparian hygrophilous forests (*RF*) are found along some small rivers (*quebradas*), *Drimys winteri*, *Salix chilensis* and *Myrceugenia* spp. being the dominant elements; the dense *Drimys winteri* forests existing on phreatic sites in very isolated situations also have similar characteristics. The montane deciduous forests (*DF*) are those of *Nothofagus obliqua* var. *macrocarpa* developed on pole-facing slopes at higher elevations in the coastal mountains, up to 2220 m (top of Cerro El Roble). The evergreen sclerophyllous forests (*SF*) with *Cryptocarya alba*, *Quillaja saponaria* and *Lithraea caustica* occur in the canyon bottoms and in some pole-facing slopes at lower elevation; great floristic and faunistic similarities exist with the matorral. The sclerophyllous shrublands (*SM*), the Chilean matorral, seem to be the climax formation of the semi-arid zone with mediterranean climate; together with evergreen species such as *Lithraea caustica*, *Kageneckia oblonga* and *Colliguaya odorifera*, some drought-deciduous and spiny shrubs (*Trevoa trinervis*, *Colletia spinosissima* and *Ephedra andina*) are usually present. The open savannas called *espinal* (*AS*) with *Acacia caven* (a deciduous phreatophyte) as dominant species, and *Prosopis chilensis* with only scattered individuals, have at present an understory where the grasses introduced from the Mediterranean Basin region are the essential component. These savannas are subject to intensive grazing pressure and are sometimes considered as a degradation stage of the matorral; however, they may well represent the climax community of the flat plains of the central valley of Chile, since there is no evidence in these situations of successional patterns towards the matorral (Rundel, Chapter 10). The montane matorral

(*MM*) occurs on the Andean slopes at elevations from some 1200 m up to more than 2000 m; in general, plants are more xeromorphic and more spiny than in the true matorral; at higher altitudes they often take a cushion-like aspect; near the quebradas, *Escallonia myrtoidea* becomes dominant. Finally, the open shrubland with succulents (*SS*) comprises both formations with *Trichocereus chiloensis* and *Puya* in the xeric equator-facing slopes of the central zone of Chile, and the coastal matorral of northern Chile with an abundance of drought-deciduous shrubs such as *Fuchsia lycioides*, *Proustia pungens* and *Adesmia arborea*; this is the formation which has probably suffered man's disturbance most strongly.

While the soil fauna of the sclerophyllous shrublands (matorral) is the main focus of this chapter, it would not be possible to understand its structural features, unless it is considered in relation to the fauna inhabiting the soils of the other more humid or more xeric formations which exist in the same zone as an ecological gradient.

A number of publications refer to some of the data included in Table 24.1 (Di Castri et al., 1961; Hermosilla, 1962; Martínez and Sánchez, 1962; Di Castri, 1963b,c; Covarrubias et al., 1964, 1965; Murúa, 1966; Hermosilla and Murúa, 1966; Hermosilla and Rubio, 1976, 1977). However, most of the data come from results of still unpublished research carried out in Chile by the authors and their co-workers. Through these surveys, nearly a million specimens of soil animals have been collected. This is the first time that a synthesis of these results is presented in a comprehensive way.

As regards the taxonomic identification of these materials, mention should be made, among others, of the following publications: Athias-Henriot (1969) for the Gamasides; Franz (1964) and Robaux (1969) for some Prostigmata; Mahunka (1968) for the Scutacaridae mites; Covarrubias (1967, 1968) for the Oribatei; Vitali-di Castri (1962, 1963, 1969a,b, 1972, 1975) for the Pseudoscorpionida; Scheller (1968) for the Pauropoda; Rapoport and Rubio (1963, 1968) and Najt and Rubio (1978) for the Collembola Arthropleona; González and Smith (1964) for the Diplura Japygidae; Badonnel (1963, 1967, 1971) for the Psocoptera; Coiffait (1963), Coiffait and Sáiz (1964, 1965, 1966, 1967, 1968) and Sáiz (1969) for the Coleoptera Staphylinidae; Jeannel (1963, 1964) for the Coleoptera Pselaphidae;

Franz (1967) for the Coleoptera Scydmaenidae; Kaszab (1969) for the Coleoptera Tenebrionidae; Bonniard de Saludo (1969) for the Coleoptera Carabidae; Dajoz (1967) for the Coleoptera Lathridiidae.

Considering the soil fauna of the eight "natural" formations (left part of Fig. 24.1), it appears that density and species diversity decrease gradually from the dense hygrophilous forests towards the more shrubby or more open formations. Values in the matorral (*SM*) are intermediate between those of the forested areas and those of the savannas and of the subdesertic ecosystems.

The riparian forest (*RF*) partly constitutes an exception, because values of density are greater and values of diversity are less than those for the hygrophilous fog forest (*FF*). This contraposition of density *versus* diversity is a normal trend in the mediterranean zone of Chile in situations where soils are subject to periodic floods, as in this case; this trend will appear in a much exaggerated form when the irrigated fields are analyzed.

In the Chilean zones with subhumid and humid mediterranean climates, the relations between hygrophilous and sclerophyllous forests are similar to those shown in Fig. 24.1 — that is, with higher values of diversity and density for the soil fauna in the hygrophilous forest. In absolute terms, diversity is high in both formations, reaching values of about five bits per individual (Montero and Christen, 1974). Similar values have been observed in the hygrophilous forests of the mediterranean perhumid region (Sáiz and Di Castri, 1971).

At a first interpretation of the information in Fig. 24.1 on this ecosystem gradient, both the organic matter and the water content of soil could be invoked as the main factors explaining the progressive decrease in density and diversity of soil fauna. Of course, no one single factor can be responsible for this trend, but rather a complex interaction of different phenomena. However, a series of correlations involving the soil fauna of different formations and at different soil depths (Di Castri et al., 1965a) demonstrated that the organic matter content of soil is the main factor influencing the distribution and the diversity of soil fauna in this region of Chile. Similar conclusions have also been reached, as regards density, from research in Italy (Di Castri and Astudillo, 1966b). On the other hand, soil moisture can influence the soil fauna both

by deficit and excess; in clay soils of low permeability, correlations between the density of mites and the water content of soil may even be negative (Di Castri and Astudillo, 1966b). Of course, the content of organic matter in soil depends largely on the density and characteristics of the vegetation, which is itself greatly influenced by water availability; this illustrates the degree of interdependence of these two factors, soil organic matter and soil water content. These aspects will be further discussed in this chapter, when the soil fauna of the five regions with a mediterranean climate are compared.

It would be out of the scope of this volume to discuss in detail the distribution and the ecological characteristics of all the soil animal groups enumerated in Table 24.1 (the sequence of ecosystems is the same as in Fig. 24.1). The most important conclusions are as follows:

(a) As regards mites (Acarina), the density of Oribatei and Uropodina decreases in a rather regular way from the forested soils towards those of open shrublands. On the contrary, the density of Prostigmata increases, reaching the maximum absolute values in the sclerophyllous (primarily evergreen) matorral, and maintaining high relative values in the xeric formations of montane matorral and open shrublands.

(b) Isopoda and Diplopoda have maximum density in the hygrophilous forests, their respective abundance alternating in the different types of hygrophilous forests (and also, within the fog forests, in different localities). They play a similar (and sometimes competing) rôle as large decomposers. In more xeric formations (sclerophyllous forest and matorral), the small and hairy Pselaphognata (Polyxenidae) are dominant among the Diplopoda.

(c) The Collembola, including the Symphypleona, have a relatively high density only in the riparian forests. In general, they have low abundance in the true mediterranean formations of central Chile, as compared with the populations of mites. The ratio mites:Collembola, which is sometimes said to be 2:1 in normal situations, is much higher in these Chilean soils.

(d) The psocids (Psocoptera) also reach progressively their highest density in the sclerophyllous matorral. They are relatively well represented in the shrublands with drought-deciduous and succulent plants. The Psocoptera fauna constitutes one of the

most typical features of the Chilean matorral, not only because of the abundance of individuals and the high species diversity, but also for its great biogeographical and ecological originality. Several new genera have been described, among them two genera of the subfamily Electrentominae (Amphientomidae) which was known before only as fossils in the Baltic amber (Badonnel, 1967); they were probably able to survive because of their adaptations (apterism, neoteny) to the soil habitat.

(e) The Protura, a strictly hygrophilous group which in hygrophilous forests inhabit mainly the litter and humus layers, also occur in xeric eco-systems, but there they occupy deeper soil strata.

(f) The endogeous beetles (Coleoptera Staphylinidae, Pselaphidae and Scydmaenidae), most of them of Paleoantarctic origin, are particularly abundant in the fog hygrophilous forests and in the deciduous forest — that is to say, in the formations having the greatest affinities with the austral Valdivian forests. They are also present, however, in the sclerophyllous forest and in some dense matorral.

(g) The soil fauna of the sclerophyllous, primarily evergreen, matorral is characterized particularly by a high density of Prostigmata, which are at least equal to the populations of Oribatei, and by the abundance of Pseudoscorpionida, Psocoptera and Thysanoptera. The populations of Collembola, and particularly of Symphypleona, are very low, at least when only the individuals in an active state are considered.

(h) The matorral soil fauna shows the greatest physiognomic resemblance and species similarity with that of the sclerophyllous forests, while affinities are low with the fauna of the *Acacia–Prosopis* savannas. The fauna of the open shrublands is a very impoverished one and contains several more xerophilous elements, but still keeps affinities with that of the matorral.

(i) In general terms, the soil fauna of the Chilean matorral belongs to the forest-type group (which embraces the first five formations of Table 24.1 and Fig. 24.1), while that of the neighboring mediter-ranean savannas (with relative abundance of Gamasides, Oribatei and Collembola) is closer to the grassland type.

Comparison with man-manipulated ecosystems in Chile

In the neighborhood of the sites where the surveys described above have been carried out, systematic sampling has been undertaken of the soil fauna of man-manipulated ecosystems along anthro-pogenic gradients (Di Castri, 1973b), in order to understand the trend of the modifications induced by man's activities, taking a "natural" situation as a benchmark for comparisons.

The results are presented on the right-hand side of Fig. 24.1 and Table 24.1. They refer to monocul-ture plantations of *Eucalyptus globulus* ssp. *globulus* (*EP*) and *Pinus radiata* (*PP*); to wheat crops grown using the dry-farming practice called in Chile *secano* (*DC*); to fields under irrigation (*IC*) with a variety of crops (mostly corn and lucerne); and to irrigated artificial pastures (*IP*) of lucerne (*Medicago sativa*) and clover (*Trifolium*) bordered by rows of *Populus* and grazed by cattle (some animals inhabiting the *Populus* litter or colonizing cow dung are thus also included here).

The type of modifications of the animal com-munities in the agricultural soils, as compared with the natural ones under mediterranean climate, have been reviewed and discussed by Di Castri (1963c, 1966, 1968) and Di Castri and Covarrubias (1966). As shown in Fig. 24.1, species diversity is lower than in any natural formation, but density is sometimes very high. It is under man-manipulated situations, and particularly in fields under irrigation practices, that a contraposition often occurs between decreas-ing species diversity and increasing density. The decrease of species diversity is not always due to a reduction in the number of species (sometimes there is even an augmentation), but rather to a "distor-tion" of the equitability component of species diversity (Lloyd and Ghelardi, 1964), a few species becoming extremely abundant in relation to the others. The indices used to measure the species diversity take into account the equitability compo-nent, their values thus decreasing when the distri-bution among species is less "equitable".

It is of particular interest to study the soil fauna under the plantations, since these tree species originate from regions which also have a mediter-ranean climate, namely *Pinus radiata* from California (with a patchy distribution from latitude 35˚30′ to 37˚ N centered in Monterey), and

Eucalyptus globulus ssp. *globulus* from southern Australia [but subspecies of *Eucalyptus globulus* are also found in Australia in regions with a slight summer maximum of rainfall (Turnbull and Pryor, 1978)]. Both species have been widely distributed by man, the areas of introduction including some under other climatic conditions, such as *Eucalyptus globulus* in the tropics (but at high altitudes), and *Pinus radiata* in New Zealand and the very rainy Valdivian zone of southern Chile. In this respect, *Eucalyptus globulus* would be an exception among the eucalypts, since, as pointed out by Turnbull and Pryor (1978), "the transfer of species from winter-rainfall areas to summer-rainfall areas is usually unsuccessful", while "there are numerous examples of the successful transfer of species from summer-rainfall areas to winter-rainfall areas". Incidentally, this fact seems to provide indirect evidence that: (a) the adaptation of eucalypts to the new winter-rainfall conditions when the mediterranean climate appeared in Australia (see Specht, 1979; Di Castri, Chapter 1, this volume) would not have constituted a major problem, and (b) several species of eucalypts have now developed features specializing them for the winter-rainfall mediterranean environment.

When comparing the two types of sclerophyllous forests in the central zone of Chile at latitude 33°S, the autochthonous formation (a natural forest with *Cryptocarya alba* and *Peumus boldus*) and the exotic one (the fast-growing *Eucalyptus* plantation), it is noticed that the overall density of soil animals and also the gross physiognomic aspect of the soil communities are very similar. On the other hand, species diversity decreases very sharply in the *Eucalyptus* plantation. This is not due primarily to the diminution of the number of species (from 94 in the natural forest to 80 in the *Eucalyptus* plantation), but mainly to the enormous increase, under *Eucalyptus*, in the abundance of two species of Oribatei and two of Collembola Poduromorpha (all present also in the "natural" soil), thus altering the equitability among species. The values of redundance (to a certain extent the opposite of equitability) increase from 0.24 in natural forest to more than double (0.53) in the *Eucalyptus* forest; these values are the highest recorded to date in the mediterranean ecosystems of Chile (Di Castri, 1973b).

From the viewpoint of soil microbiology too,

there are several similarities between the two forests, particularly in the number of Actinomycetes and of aerobic bacteria. The numbers of anaerobic bacteria decrease slightly in the *Eucalyptus* forest, but the anaerobic *Clostridium* remains as the principal nitrogen fixer, while *Azotobacter* is absent in both natural and man-made situations; denitrification is very rapid in both forests. Only the number of soil fungi falls very markedly under *Eucalyptus*. In soils of Morocco under plantations of *Eucalyptus camaldulensis* and *E. gomphocephala*, Pochon et al. (1959) noted the absence of *Clostridium* and a very strong mineralization of organic matter with little production of humus.

Drastic changes happen, on the other hand, in the biological conditions of the soil under *Pinus radiata* plantations, in spite of the fact that they were at no more than 100 m distance from the natural formations and the *Eucalyptus* plantations. The species diversity of soil animals is the lowest of those depicted in Fig. 24.1; the number of individuals of soil animals decreases by a factor of seven, the number of species is halved, and the number of aerobic bacteria is only one-fifteenth of that in the natural situation. Only the numbers of Actinomycetes and anaerobic bacteria remain almost unchanged (G. Franz, 1968, unpublished data), and the numbers of soil fungi increase (to almost three times those found under the *Eucalyptus* plantation). Denitrification becomes very slow.

It is suggestive that in the central zone of Chile, unlike the Mediterranean Basin areas, there are no native conifer formations, with the exception of some very isolated stands of *Austrocedrus chilensis* in the high Cordillera (Schlegel, 1962). It seems that these Chilean mediterranean soils were not adapted, from a biological point of view, to developing a coniferous plant cover without dramatic structural and functional changes.

South of this region, in the subhumid and humid mediterranean-climate zones, the differences in soil zoology between plantations of *Eucalyptus* and of *Pinus radiata* are much less marked, but still with more favorable conditions for the soil fauna under *Eucalyptus* (Montero and Christen, 1974). In the rainy Valdivian region, some plantations of *Pinus radiata*, in spite of the further acidification of soil, show values of animal species diversity almost as high as those of the natural formations (Sáiz and Di Castri, 1971). Therefore, the biological status of the

soil under *Pinus radiata* plantations seems to improve towards the moister (but still temperate) parts of the latitudinal gradient. This is in accordance with the forestry productivity of these plantations, whose maximum in Chile occurs in the regions with a perhumid mediterranean climate or a rainy oceanic climate with the rainfall peak still in the winter. In these regions, growth of *Pinus radiata* is extremely rapid, attaining in favorable situations 45 m³ ha⁻¹ yr⁻¹ — that is, ten times more than the native formation (values in the native forest of the same region of Chile are only 3 to 4 m³), and certainly much more than in the area of natural distribution of *Pinus radiata* in California (Matte, 1971).

As regards the other man-manipulated ecosystems (*DC, IC* and *IP* in Fig. 24.1), the dry-land wheat fields have a soil fauna which resembles that of the xeric open shrublands in species diversity, number of individuals and faunistic similarity. The numbers of Acaridiae mites increase as in all arable lands of the central zone of Chile (Di Castri, 1963c), and the Thysanoptera are particularly abundant in the superficial layer of wheat straw.

A complete disarrangement of the previous community structure occurs, on the contrary, in the soil of fields under irrigation, particularly when irrigation practices are somewhat equivalent to periodic floods, as the so-called *riego tendido* (flood irrigation) of the pastures. The major changes, as compared with the natural situation, are the following:

(a) A great decrease in species diversity, due to the elimination of numerous humicolous species (living in humus and litter), and to a great increase in the population density of a few species of Acaridiae mites, springtails (Collembola) and, to a lesser extent, Gamasides mites.

(b) Generally high and very variable total density of soil animals. Data given in Table 24.1 represent an average, and densities of 13 500 specimens or more per dm³ of soil have been recorded in the mediterranean region (Di Castri and Covarrubias, 1965); the absolute maximum of animal density in Chilean soils (40 304 specimens in 1 dm³ soil) occurred in an irrigated grassland in the Norte Grande, Atacama Desert (Di Castri, 1963c).

(c) Almost complete disappearance of groups such as pseudoscorpions and Uropodina mites (very sensitive to human intervention, and/or

linked to the presence of particular types of humus), and of the strictly edaphic (eu-edaphic) beetles (Staphylinidae Leptotyphlinae, Pselaphidae) which are unable to endure anaerobic conditions during irrigation.

(d) Frequent vertical migrations in the soil profile of hygrophilous aerobic groups such as the Pauropoda and particularly the Protura, following the irrigation rhythms, and in accordance with the excess or the deficit of soil moisture. Even the very rare group of Palpigrada has been found at great depth in the irrigated fields of central Chile (*Eukoenenia mirabilis*, Condé, 1974).

(e) Decrease of the ratio predator:consumer species according to the Volterra–D'Ancona laws (Di Castri, 1963c).

(f) Very strong decrease of the ratio Oribatei:Acaridiae mites, which has been proposed by Di Castri (1963c) as a good index for measuring the degree of human intervention in soils of the mediterranean zone of Chile. The ratio is about 6 to 7 in the natural formations (up to 32 in the fog hygrophilous forest), decreases to about 3 when man's impact becomes greater as in the *Acacia* savanna and in the scattered shrublands, and falls below 1 in the arable lands (0.9 in the dry fields and even less than 0.1 in the irrigated fields).

In the perarid mediterranean zone (see Di Castri, Chapter 1), the effects of irrigation are different, since it acts on sandy desertic soils which were almost completely azoic before the irrigation practices began. Density and species diversity regularly increase as the number of years of irrigation becomes greater, but the values reached are still very low. During the first years of irrigation soils are colonized mainly by phytophagous and saprophagous species of arthropods, but in the following years predatory species appear (Di Castri and Vitali-di Castri, 1971).

In the subhumid mediterranean region, Montero and Christen (1974) undertook similar research on the soil fauna of cultivated fields with comparable results to those discussed above. Wheat fields represent relatively little modified conditions, followed by vineyards and fruit plantations, some annual crops such as sugar beet and sunflowers (where pesticides have a depressing effect on the soil fauna), and finally rice fields where the lowest values of species diversity and density of all the agricultural soils of Chile have been found; in this crop, the

effect of pesticides is associated with long flooding periods.

Comparison with other mediterranean-climate regions

Comparisons between Chile and the other regions of the world with a mediterranean climate, as regards the soil fauna, are admittedly very arduous, and not only for the three main reasons evoked in the first part of this chapter (lack of taxonomic knowledge, differences in methods of extraction, differences in approaches). In fact, with the exception of Chile, surveys on the structure of soil animal communities have not been conducted in a comprehensive way so as to cover all ecosystem types (both natural and man-modified) and most of the animal groups, in a multiplicity of sites and ecological situations.

The inter-regional comparisons made in this chapter, therefore, will be mostly confined to the results of investigations from the few sites where intensive research has been carried out during some months or in an annual cycle. On the other hand, long-range investigations in Chile on soil fauna have demonstrated how great is the inter-site heterogeneity, even within a given region, and how important are the differences between successive years, because of the mosaic-like variety of microhabitats in the mediterranean landscape and of the seasonal and inter-annual variability of the mediterranean climate. These limitations must be kept in mind when considering the conclusions drawn from these comparisons.

The comparisons are based on a number of publications which have been selected mainly on account of the degree of comparability with the research carried out in Chile, as regards methods and animal groups. Taxonomic or primarily auto-ecological investigations are not included in the following bibliographical review. For the Mediterranean Basin region, mention should be made of the publications of Di Castri (1960, 1963c), Cassagneau (1961), Di Castri and Astudillo (1965, 1966b), Lions (1966, 1975, 1977), Marcuzzi (1966, 1968), Marcuzzi and Di Castri (1967), Marcuzzi et al. (1970), Poinsot-Balaguer (1971, 1976a), Marcuzzi and Dalla Venezia (1972), Bigot and Bodot (1972), Alicata et al. (1972, 1973), Motta and Petralia

(1973), and Vannier (in Lossaint and Rapp, 1978), some of them dealing with the northern limits of the mediterranean climate; for California, to Wallwork (1972) which includes sites with a non-mediterranean climate, and Di Castri (1973b, and unpublished data); for South Africa, to Lawrence (1953), Olivier and Ryke (1965), Den Heyer and Ryke (1966), Loots and Ryke (1966, 1967) and Van den Berg and Ryke (1968), though most research refers to summer-rainfall localities; for Australia, to Wood (1970, 1971) whose investigations deal mostly with desert sites, Greenslade and Greenslade (1973), Greenslade (1974, 1975) and Edmonds and Specht (1980).

In general terms, the structural patterns of soil animal communities which, at the present state of knowledge, seem to be common to all the five regions with a mediterranean climate are the following:

(1) As regards the phenology, the seasonal peak of density is in the winter (Wood, 1971; Alicata et al., 1973), or more frequently there are two peaks (Marcuzzi, 1968; Wallwork, 1972; Edmonds and Specht, 1980), one in spring and the other in autumn (or in winter), with a minimum in summer. For instance, only a few species of mites have their maximum density in the summer (Alicata et al., 1973). It is interesting to note that the maximum of population density is also typically in winter in some regions of South Africa where rainfall is concentrated in the summer (Van den Berg and Ryke, 1968). In this respect, it could be postulated that the transition from tropical conditions to the mediterranean climate in the Pleistocene (Axelrod, 1973) might not have implied dramatic changes in the phenological adaptations of the soil fauna. Only a slight seasonality of the total density of soil meso-fauna has been observed by Ghabbour (1979) in very arid ecosystems of northern Egypt; this is mainly due to the fact that, while some species persist all the year round (with fluctuation of their density), other taxa appear only in one or two consecutive seasons and are replaced by other species when they disappear. Accordingly, the sum of species having different seasonal rhythms may well hide the phenomenon of seasonality when the overall soil mesofauna is considered.

(2) During the summer drought, a number of soil animal groups and species remain active although their density decreases, but several others survive in

an inactive state by entering into **aestivation** (Di Castri, 1973c; Edmonds and Specht, 1980). Protozoa, rotifers and nematodes encyst; some earthworms move downwards into the subsoil (Edmonds and Specht, 1980) and there aestivate; some Collembola of the genus *Sphaeridia*, and probably of several other genera, seem to pass most of the summer as desiccation-resistant eggs (Poinsot-Balaguer, 1976a). A most interesting and peculiar type of aestivation is that described by Poinsot-Balaguer (1971, 1974, 1976a) in southern France and Tunisia, and by Wood (1971), Greenslade and Greenslade (1973) and Greenslade (1974, 1975) in southern Australia: among the Collembola, some species of the genera *Folsomides* (*F. variabilis* in the Mediterranean Basin, *F. deserticola* and *F. sexophthalma* in Australia) and *Brachystomella* are able to overcome the dry season as adults in an inactive state of anhydrobiosis. Even occasional summer showers, which occur in southern Australia as well as in the French Provence, can re-activate these aestivating adults (Greenslade, 1974, 1975). Heavier effective rains seem to be necessary for stimulating the eclosion of *Sphaeridia* eggs and then the reproductive processes of these Collembola in a very short life cycle (Greenslade, 1975). Similar results can be obtained in the laboratory by moistening the soil samples (Poinsot-Balaguer, 1976a). It is not known to what extent this phenomenon occurs also in the other mediterranean-climate regions, since the methods of extraction which permit one to collect or to re-activate dormant forms (flotation processes or extraction by Berlese–Tullgren after moistening the samples) have not been widely applied in these regions. It would be certainly worth undertaking this line of research in the arid and mediterranean zones of Chile and California.

(3) Soil animal populations are not randomly distributed, but usually occur in aggregates (Di Castri and Astudillo, 1965, 1966b; Astudillo et al., 1966; Den Heyer and Ryke, 1966; Alicata et al., 1973), the degree of aggregation increasing in accordance with the population density. This phenomenon does not seem to be peculiar to mediterranean soil fauna, but it is probably accentuated in the mediterranean environment because of its greater heterogeneity.

(4) The density of Prostigmata mites increases towards the xeric parts of the environmental gra-dients, and in dry formations exceeds the density of Oribatei mites (Di Castri, 1963b; Van den Berg and Ryke, 1968; Wood, 1971). On the other hand, Oribatei dominate in forest soils with a high content of organic matter. Accordingly, Covarrubias et al. (1964) proposed an index or ratio Oribatei:Prostigmata, largely equivalent to Oribatei:Trombidiformes (Loots and Ryke, 1967) or Cryptostigmata:Prostigmata (Wallwork, 1976); this ratio characterizes the degree of xerophily of the acarofauna (and in general of the soil animal community) of a given soil. For instance, in Chilean soils with a mediterranean climate (see Table 24.1), this ratio decreases from 25 in the hygrophilous forest, to 3.2 in the deciduous forest, 1.4 in the sclerophyllous forest, 0.9 in the sclerophyllous matorral, 0.6 in the open coastal shrubland and only 0.15 in the montane matorral. Loots and Ryke (1967) demonstrated for South African soils that the variations of the values of this ratio are directly correlated with the soil organic matter content, and that "soil water content as such is not always the most important factor in determining the composition of the acarofauna". This is totally in agreement with what has been stated here about Chilean soils, and with the results of Di Castri and Astudillo (1966b) for Italian soils.

(5) Among the dominant groups, mites are normally more abundant than springtails (Collembola) in the mediterranean soils, in a proportion exceeding the ratio 2:1 which seems to prevail in temperate soils (Marcuzzi and Dalla Venezia, 1972). The exception seems to be Australia, where the occurrence of large populations of Collembola (mostly Isotomidae and Poduroidea) has been indicated not only in shrublands (Greenslade, 1975), but also in deserts (Wood, 1970, 1971), sometimes equalling or outnumbering the populations of mites; however, it is difficult to evaluate to what extent the different methods of collection (flotation, extraction from dry or moistened samples) are responsible for these dissimilarities. At the other extreme, it seems that the average density of Collembola is lower in Chile than in any other mediterranean-climate region. In any case, Collembola react much more quickly than mites, through important fluctuations of their population density (dying or aestivating in unfavorable situations, initiating rapid reproduction processes in favorable situations), to environmental changes and particularly to changes in soil moisture

(Di Castri and Astudillo, 1966b). It seems that, in a comparative way and taking into account the relativity of these concepts (see Pianka, 1970), most species of Collembola have an evolutionary position close to the *r*-selection type, while some species of mites (mostly of Uropodina and Oribatei) approach a *K*-selection type, with slower development and more stable populations.

(6) Very frequent vertical migrations of soil animals take place between the litter and the deeper soil in response to changes of soil moisture, following the occurrence of rainfall and drought periods (Alicata et al., 1973; Di Castri, 1973b; Motta and Petralia, 1973). Ghabbour (1979) found that, even at the most arid margins of the mediterranean climate in northern Egypt, the deeper soil layers (at 50 cm) present a relative humidity of 100% for most of the year; the available water at depth provides mobile soil animals with a refuge when adverse conditions prevail in the topsoil. Methodologically, this implies, in a mediterranean environment, that studying only the superficial soil layers would lead to incomplete results and to incorrect conclusions; in general, systematic sampling at least to 30 cm depth would be advisable, since some groups (Protura, Japygoidea, some Gamasides, some small endogeous beetles) are found only at such depths during the drought period (Covarrubias et al., 1964).

(7) As regards stratification, the greatest density under sclerophyllous formations is sometimes found in the litter (Alicata et al., 1973), sometimes in the underlying humus layer (Lions, 1966); obviously, the patterns of stratification vary with the vertical migrations of soil animals. Species diversity is usually higher in the humus than in the litter, and shows greater seasonal fluctuations in the litter than at depth; at least the equitability component of species diversity increases towards the deeper horizons (Lions, 1977).

(8) The content of organic matter in soil and the water availability in soil have both been evoked in this chapter, through different quotations, as the key ecological factors controlling the dynamics of soil animal populations under mediterranean climates. As already stated, these two factors are interconnected to a certain extent, and their relative importance depends somewhat on the different perspectives of the investigators. In synthesis, the varying content of organic matter in soil, from site to site, is primarily responsible for the differences in species distribution, species diversity and community structure of the soil fauna. The seasonal changes in water availability, on the other hand, are the chief factor in inducing population changes (population outbreak or decline, vertical migrations) within a given site. Usually, increasing soil moisture stimulates the population densities very positively (specially of Collembola), but an excess of water in clay soils poor in humus lowers the species diversity and often the density, especially of mites (Di Castri and Astudillo, 1966b; Lions, 1977). In studying the soil fauna under *Quercus ilex* in southern France, Vannier (in Lossaint and Rapp, 1978) postulates the "independence" of Oribatei mites and Collembola (Isotomidae and Poduromorpha) vis-à-vis the water variations in soil. Though this statement may be applicable to the favorable conditions of the research site (a forest at the northern limit of the mediterranean climate) and of the year of sampling (the wilting point occurred only on one day during that year), it cannot be generalized to other types of mediterranean soils and climates. On the other hand, Vannier points out very rightly that what is of importance to the soil invertebrates is not the absolute amount of water in the soil, but its availability, expressed as pF — the "water accessibility" according to Vannier (1970). "The animals are only affected by the desiccation of their substrate beyond a critical threshold of the humidity level, which is constant for each group of species. This critical threshold testifies to the force of retention which is exerted by solid matter on water, and which the animal is eventually unable to overcome" (Vannier, 1970, p. 247). This threshold is generally situated around the permanent wilting point (pF 4.2), and the Collembola seem to be more sensitive to a decrease in the water availability in soil than most of the mites (Di Castri and Astudillo, 1966b; Vannier, 1970).

For the following aspects, the interpretation of results is more controversial, or the scantiness of available information does not permit reliable generalizations:

(a) As regards levels of species diversity, some comparable data exist for California and Chile (Di Castri, 1973b). Species diversity at the site level (α diversity) seems to be slightly higher in Chile, while the number of species is greater in California. This apparent contradiction is due to the fact that the

equitability among species is higher in Chile, and that redundance (great abundance of few species) is more marked in California than in Chile. However, when considering the accumulated diversity (somewhat equivalent to the β diversity), the differences between these two regions decrease, and at the level of maximum diversity (Di Castri, 1973b) the values are almost identical.

(b) Density is a much less stable parameter; in addition, some authors express it in units of volume, others in terms of area.

Two inter-regional studies comparing Italy and Chile on the one hand (Di Castri, 1963c), and Chile and California on the other (Di Castri, 1973b), seem to support the impression that density of soil animals is generally lower in Chile than in the two mediterranean-climate zones of the Northern Hemisphere. As a rule, density in all the arid mediterranean ecosystems is lower than in the neighboring more humid and temperate zones with forested soils, as for instance at the poleward margins of the mediterranean climates.

(c) The psocids do not seem to have as important and peculiar a rôle in the maquis formations of the Mediterranean Basin (Marcuzzi, 1968) as that which they play in the Chilean matorral. Some research on this group has been carried out in southern France (Guillaumont, 1977). It is interesting to note that, in a mediterranean formation of southern France experimentally submitted to chronic gamma irradiation, an enormous demographic outbreak of psocids has been observed (Bigot et al., 1973; Poinsot-Balaguer, 1975a, 1976b), due perhaps to the proliferation of terrestrial algae (some of the psocids are algophagous, others saprophagous) and/or to the elimination of their predators, parasites and competitors.

(d) Among other physiognomic differences, it can be underlined that Protura are apparently more abundant in the mediterranean regions of the Northern Hemisphere than in Chile (Di Castri, 1963c), and that the Copepoda adapted to a terrestrial life are more frequent in Australia (Wood, 1970, 1971) and in Chile (Löffler, 1966) than in the mediterranean soils of the Northern Hemisphere.

(e) The soil fauna under coniferous formations, such as *Pinus halepensis* in Italy (Marcuzzi, 1968), has in general a lower density and diversity than under sclerophyllous shrublands.

(f) Near the brackish mediterranean wetlands of southern France, the populations of soil fauna (mostly Collembola) are concentrated on biotopes protected from the rise of temporary waters (Poinsot-Balaguer, 1975b). When the water level retreats, they colonize the empty areas, but they are limited by the varying salt content in soil, even where the soil-moisture levels would be in accordance with their ecological preferences.

(g) The number of species and individuals of soil animals can decrease with elevation as in Italy (Marcuzzi, 1966), or increase (together with the plant diversity) as in the coastal mountains of central Chile.

(h) At the present state of knowledge, no comparisons can be made as regards the biomass and the productivity of soil animals in mediterranean-climate zones.

The greatest differences between mediterranean faunas seem to refer particularly to the Australian fauna. The abundance of Collembola, even in desertic areas (with dominance of *Folsomides deserticola*), is a very striking feature, as well as the relatively high density of Crustacea Copepoda and Cladocera (Wood, 1970). However, some of the differences can, to a considerable extent, be ascribed to the extraction method by flotation adopted by Wood (1970, 1971). This method, unlike extraction of unwetted samples by the Berlese–Tullgren method, allows dormant specimens, in an inactive state because of the drought, also to be collected. Similarly, some Collembola, such as *Sphaeridia* spp., which cannot be obtained by the usual dry extraction by means of Berlese–Tullgren funnels, appear in the collections (initially immature, and after 3 to 5 days adult specimens) when samples are thoroughly moistened before extraction (Greenslade, 1975).

Another peculiarity of the southern Australian fauna deals with the scarcity of true endogeous (eu-edaphic) beetles, such as those collected so frequently in the soils of the other mediterranean-climate regions (Coiffait, 1962, 1964, 1970; Sáiz, 1973). Perhaps these beetles have not been searched for systematically, but it is likely that the flatter, nutrient-poor and sometimes podzolized Australian soils are not suitable for these very old and strictly specialized soil species, particularly if the Australian soils have been submitted to extensive flooding and waterlogging in geological times.

Finally, as regards the soils of southern Australia,

it would be of the greatest interest to undertake comparative research on the soil fauna and micro-flora existing in oligotrophic and relatively richer soils, which support respectively heathlands and sclerophyllous shrubland vegetation under the same mediterranean-climate conditions (Specht, 1979). For instance, the soil fauna of the heathlands of southern Australia described by Edmonds and Specht (1980) shows apparently much greater simi-larities with the soil fauna of the Chilean matorral, which has a similar climate but richer soils, than with the soil fauna of the temperate heathlands of Europe (Wallwork, 1976), which have a very differ-ent climate but more comparable soil conditions. In particular, the rhythm of litter decomposition with maxima in spring and autumn is the same in South Australia and Chile, and the ratio Oribatei:Prostigmata is identical (0.9) in soil sam-ples from the Australian heathland and the Chilean matorral.

In conclusion, and in spite of the paragraph above, convergences among the soil fauna of the five regions of the world with a mediterranean climate are less evident than those found in the vegetation and some animal groups such as birds and lizards (Di Castri and Mooney, 1973; Mooney, 1977; Cody and Mooney, 1978). This is not surpris-ing when one considers that the soil fauna is very old and "conservative" in geological terms, and that the deep soil environment has a number of "filters" (vegetation, litter, and humus layer) dampening the effects of the present-day seasonal climate (Di Castri, 1973a).

Soil microfauna, soil macrofauna and epigeal fauna

The previous sections of this chapter have dealt almost exclusively with the soil animals, extracted chiefly by means of Berlese–Tullgren funnels, which are conventionally called the soil mesofauna. It is the only faunistic component of the soil for which comparable investigations at the community level are now available for the five regions with a mediterranean climate.

As already mentioned, several other animal groups exist in soil: those belonging to the soil "water" microfauna (the soil aquatic animals such as protozoans, rotifers, tardigrades, nematodes), smaller but far more numerous than the mesofauna

as regards overall density; and the larger animals (soil macrofauna and megafauna), some of them living almost constantly in the soil environment such as the earthworms, other colonizing the soil only during a part of their life cycle (such as the larvae of large beetles and of Lepidoptera), or moving from the soil to the ground surface and *vice versa* such as the millipedes, centipedes, woodlice and several families of beetles, as well as some social insects (termites, ants). The so-called epigeal (or epigeous) fauna — that is, the animals of the ground surface which are usually collected by means of pitfall traps [for methods of capture, see Balogh (1958) and Le Berre (1969)], has too many groups (and species) in common with the soil macrofauna to be considered in isolation.

The following remarks, which are by no means intended to treat these groups exhaustively, can be made:

(1) The soil "water" animals are very common and numerous in mediterranean soils, including those of the arid mediterranean regions, since they are able to survive the summer drought in an encysted state. They have in general a very wide distribution (within a given region and among regions), because the cysts can be easily dispersed by winds or accidentally transported by man in dry soil and dust. In spite of this, the Testacea (Protozoa) are good ecological indicators of soil conditions (Bonnet, 1959, 1964; Bamforth, 1971; Couteaux, 1975), and their distribution in several Chilean ecosystems has been discussed by Bonnet (1966). Several species of tardigrades also have a very restricted distribution (Ramazzotti, 1962a) and provide important information from a biogeo-graphical viewpoint; most of them inhabit mosses and lichens, but there are also soil-living species; in a survey of the Chilean tardigrade fauna a number of new species have been described (Ramazzotti, 1962b, 1964a, b, 1965). Nematodes are present in Chile in all mediterranean formations, including the more arid and scattered shrublands; their density increases in irrigated fields (Covarrubias et al., 1964), where they sometimes cause serious damage to the crops.

(2) The earthworms are the most important group of soil animals from a functional viewpoint, since they constitute most of the soil fauna biomass and are extremely active in litter ingestion and degradation, as well as in the soil aeration and in the

redistribution of organic matter through the soil profile, thanks to their deep vertical migrations. The biomass of earthworms in some mediterranean soils of France has been measured by Bouché (1975), who stressed the activity of a giant species (*Scherotheca monspessulensis*) in the ingestion of coriaceous leaves of *Quercus ilex* and other sclerophyllous plants; "epigeous" species of earthworms seem to be absent in these soils. According to Bouché (1975), the planting of conifers depresses the activity and migrations of earthworms. For South Australian species of Megascolecidae, excretory adaptations favoring water conservation during the dry season have been described by Jamieson (1974).

(3) Termites are present in all mediterranean-climate regions, but their importance is much lower than in tropical ecosystems. The rôle of *Nasutitermes exitiosus* in the cycling of organic matter in mediterranean-climate formations of South Australia has been studied by Lee and Wood (1968). Di Castri (1970, unpublished data) noticed that termites are more frequent in southern California than in central Chile. In general terms, the importance of termites in mediterranean-climate regions decreases from South Africa and Australia, to California, the Mediterranean Basin and Chile, as the mediterranean climate becomes more isolated from tropical summer-rainfall influences (Di Castri, Chapter 1).

(4) A detailed intercontinental comparison of the ant fauna has been carried out between the mediterranean-climate regions of California and Chile (Hunt, 1977). The patterns of distribution of ant species along an altitudinal gradient of 2000 m are similar in the two regions. In both cases, woodland species and species from open and disturbed sites are recognizable. However, in California there exist ecological types which are not represented (honeydew-feeding species) or scarcely represented (seed-gatherers) in Chile; this corroborates the statement that in general the Chilean fauna and flora are less specialized than those of California (Di Castri, Chapter 1). In addition, both biomass and number of species of ants are clearly higher in California than in Chile.

(5) The ground-surface fauna (*epigaion*) has been extensively studied in mediterranean Chile by Noodt et al. (1962) and Sáiz (1963a,b), using Barber pitfalls (see Balogh, 1958), in some of the same sites

and ecosystem types (from the hygrophilous forests up to the open shrublands and the montane formations) where the investigations on the true soil fauna discussed earlier in this chapter were performed. In the matorral and *Acacia* savanna, there are two peaks of animal density for most of the groups: the highest peak is in the spring, with a secondary one in the autumn. In the hygrophilous forests, the seasonal fluctuations of animal density are dampened in relation to the other ecosystems. In general, the number of species and individuals in the Chilean formations is low as compared with the results of similar research carried out in temperate Europe (Noodt, 1961). Sáiz (1977) compared the ground fauna of beetles in California and Chile; this fauna is characterized in both regions by the dominance of four groups of beetles: Carabidae, Curculionidae, Staphylinidae, and Tenebrionidae; this last group represents 90% of the biomass of the epigeal beetles in the Californian chaparral, much less in the Chilean matorral. The Tenebrionidae constitute a fundamentally xerophilous group, very well represented in all mediterranean regions, as well as in the adjacent deserts; Marcuzzi (1951) stressed their importance as ecological indicators of xeric gradients. Among other xerophilous groups of the *epigaion* in the matorral, Thysanura and Solifugae (Kraus, 1966) should be mentioned. Among the hygrophilous groups found in the mediterranean region of Chile, the terrestrial planarians (Froehlich, 1967) and the Onychophora are the most interesting from a biogeographical viewpoint; both groups have a typically austral distribution (South America, South Africa, Australasia), and are now mainly localized in the moist tropical and subtropical forests (Wallwork, 1976).

Relationships with the soil microflora

It would be beyond the scope of this chapter to discuss in detail the microflora (bacteria, Actinomycetes, fungi) of soils under mediterranean climates. Some of the main microbiological trends have been summarized in a preliminary way by Schaefer (1973); monographic studies exist for Morocco (Sasson, 1967) and Chile (ONU–MINAGRI, 1970).

Most of the microbial populations are found around the plant roots in the rhizosphere. The seasonal maximum of microbial density in mediter-

ranean-climate soils has been recorded in the spring by Sasson (1967) in Morocco, in the winter by G. Franz (1969, pers. comm.) in northern and central Chile, while Schaefer (1973) reports two flushes of activity in spring and autumn, with levels of activity remaining moderate during the winter. On the other hand, Sasson and Daste (1963) described an intrinsic seasonal periodicity, especially of *Azotobacter*, not even modified by irrigation or other cultivation practices. All authors agree in finding that the minimum microbial activity under mediterranean climate is in the summer. During the dry period, most microbes adopt adaptive strategies (latent state as spores and cysts, greater concentration at depth) similar to the aestivation of soil animals; in particular, the soil "water" microfauna shares several patterns of community dynamics with the soil microflora. Microbial density in central Chile decreases in cultivated fields as compared with the natural situation (Medina, 1967), but irrigation practices increase the number of bacteria, especially of *Azotobacter*. The results of surveys carried out by Franz in Chile (Franz and Medina, 1968; G. Franz, 1969, unpublished data) are of particular interest, since they refer specifically to some of the research sites and ecosystem types whose soil fauna has been illustrated in Fig. 24.1 and Table 24.1.

In the soil of the xeric and scattered shrublands and of the dry savannas, there is a clear dominance of aerobic sporulated bacteria and of *Aspergillus* spp., particularly *A. fumigatus, A. flavus, A. ustus* and *A. wentii*. It must be noted that Loub (1963) found *A. fumigatus, A. flavus* and *A. ustus* in the Sahara, and Ranzoni (1968) isolated *A. fumigatus* and *A. wentii* from soils of the Sonoran Desert. The Actinomycetes are also a very important component of the microflora of these xeric Chilean ecosystems. *Azotobacter* is the principal nitrogen fixer. The period of maximum microbial activity, including cellulolysis and denitrification, occurs a month after the first rainfall following the long summer drought, and activity remains high throughout the winter.

In the dense forests with a mediterranean humid and perhumid climate of southern Chile, the proportion of anaerobic bacteria increases sharply, particularly during the winter. Fungi are abundant, with the exception of *Aspergillus* which is almost completely absent, while the Mucoraceae *Circinella* and *Zygorhynchus* become the characteristic ele-

ments among the soil fungi. The genus *Penicillium* occurs in both the arid and the humid ecosystems, but is represented by different species. The Actinomycetes decrease considerably in comparison with the more arid zones. *Clostridium* is the main nitrogen fixer, while *Azotobacter* is found only occasionally.

In the sclerophyllous formations of the central zone of Chile, the soil microflora shows intermediate conditions between that of the more arid and the more humid ecosystems. Fungi reach here their highest species diversity, being represented by a mixture of both xerophilous and hygrophilous elements. The aerobic sporulated bacteria decrease as compared with the more arid soils, but the Actinomycetes retain a very high density. As regards the nitrogen fixers, *Clostridium* dominates in the soils of sclerophyllous forests, while *Azotobacter* is more abundant in open areas and particularly in cultivated fields. In general, the density of soil microflora in the sclerophyllous forests is higher at a depth of 25 to 30 cm than in the top 5 cm.

The transitional position of the central mediterranean-climate region of Chile, able to retain elements from desertic as well as from moist temperate zones, in addition to its peculiar species, is therefore confirmed also in relation to the soil microflora.

Relationships with plants

Most of the previous discussions have dealt with soil animal communities in relation to given plant formations along environmental gradients. In this respect, there is no correlation between the plant species diversity of a formation and the species diversity and density of the corresponding community of soil animals. For instance, the deciduous forest dominated by only one species of *Nothofagus* (see Fig. 24.1 and Table 24.1) has a soil fauna with higher species diversity (and also density) than that of the sclerophyllous forest where the overstory comprises several tree species. The main factors for the soil fauna are the plant cover and, above all, the amount and the quality of the litter.

However, at another scale of observation — at the level of a research site or of a sequence of neighboring sites within the same ecosystem type — some correlation between number of species of plants and of soil animals can be demonstrated. This is illustrated in Fig. 24.2, which refers to a zone

of subalpine hills near Vicenza (Italy) at the northern limits of the mediterranean climate (Di Castri, 1960). The following conclusions can be drawn:

(1) The number of species of soil animals largely exceeds that of plant species in the above-ground subsystem (and the number of soil animal species in Fig. 24.2 represents only a part of the community, since only the individuals properly identified at a known species level are recorded here). The number of species of animals at different points up an elevation gradient, on both the calcareous and the volcanic substrates, is directely correlated with the number of plant species present.

(2) Soil animals seem to be more dependent than plants on the geological substrate, and they show a higher "fidelity". Calcareous rocks, deeply fractured and producing more permeable (and less clayey) soils, consistently support a richer soil fauna throughout the altitudinal gradient, in spite of different degrees of human impact which affect the diversity and species composition of plants more substantially. The soil subsystem, therefore, seems to be more stable in geological and ecological terms than the above-ground subsystem.

A LATITUDINAL GRADIENT OF SOIL ANIMAL COMMUNITIES

The research on the soil fauna carried out by the authors and numerous collaborators from 1960 up to 1971 was not restricted to the mediterranean-climate zone of Chile *sensu lato*, but covered also areas of the Atacama Desert and of the high Andes (Di Castri et al., 1965b; Di Castri and Vitali-di Castri, 1971), of Valdivian temperate rain forests (Sáiz and Di Castri, 1971), of Pacific Islands (Zeiss, 1967; Rubio and Hermosilla, 1971) and of Magellanic forests and moorlands (Rubio, 1974), as well as tropical forests in Paraguay and Brazil (Hermosilla et al., 1967), and polar deserts in Antarctica (Covarrubias, 1966; Di Castri et al., 1970).

This constitutes an almost continuous' north–south gradient of about 7000 km, embracing all types of ecosystems (both natural and man-modified) and of climatic zones. Some very preliminary results have been published by Di Castri (1969). This latitudinal transect is comparable only to that studied in the Soviet Union by Ghilarov and
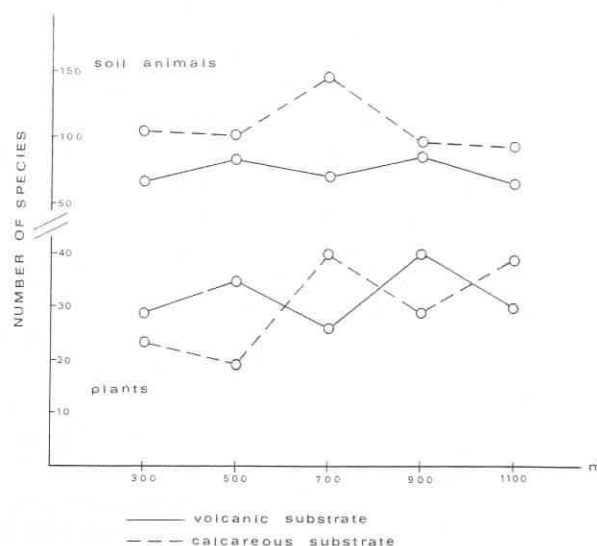

Fig. 24.2. Number of species of plants and of soil animals in correspondence to two geological substrates and five altitudinal steps in Italy.

his assistants (see Ghilarov, 1964, 1965), from the tundra to the deserts of Central Asia and up to the subtropical forests of Transcaucasia. In particular, the "rule of the zonal change of strata", formulated by Ghilarov, is fully confirmed by the results of research performed along this environmental gradient from the South American tropics up to Antarctica. This rule postulates that the soil-related animals change their vertical position in the ecosystems, from the suspended soils on branches of tropical trees at 50 m height (see Delamare Deboutteville, 1951) down to very deep soil, in response to different environmental conditions such as moisture saturation of the air, soil drainage and aeration, seasonal droughts, rigorous winter, etc.

Within the framework of this volume, it is only intended in this chapter to place the soil fauna of mediterranean-climate soils within the perspective provided by two extreme ecological situations, those of the tropical and of the antarctic ecosystems. Three community features — aggregation, diversity and stratification — have been chosen to illustrate this latitudinal comparison of soil faunas (Figs. 24.3, 24.4 and 24.5).

Ranges of aggregation values for soil arthropod populations (mostly Collembola) in the tropics, in the mediterranean-climate region of central Chile and in Antarctica are presented in Fig. 24.3. For further information on the aggregation of soil
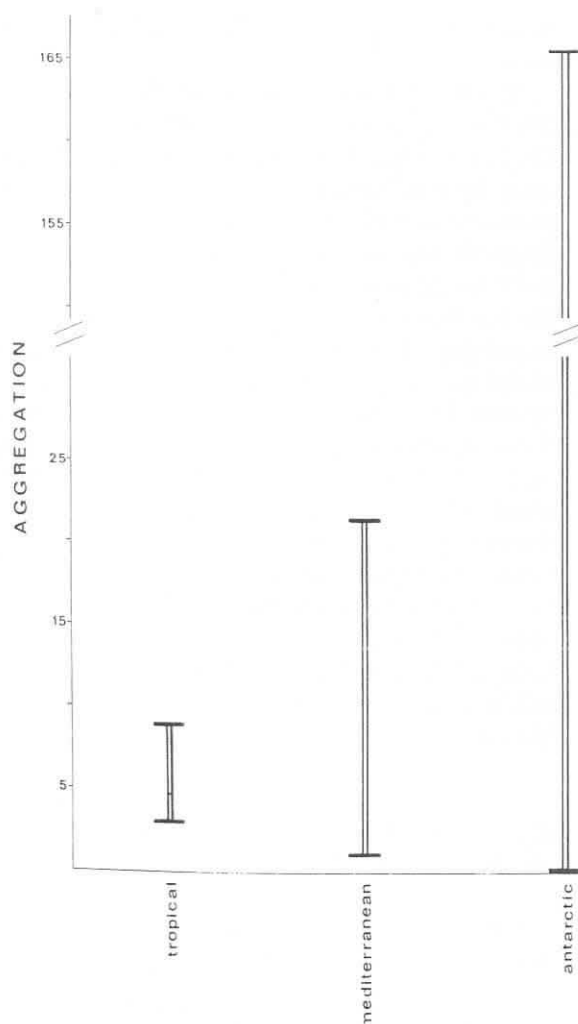
Fig. 24.3. Range of aggregation values of soil arthropod populations in the tropics (Brazil and Paraguay), in the mediterranean-climate zone of Chile and in Antarctica (South Shetland Islands).

animal populations, reference is made to Debauche (1962), Astudillo et al. (1966), and Vannier and Cancela da Fonseca (1966). In the most favorable situation, the tropical one, the aggregation values are low and stable; the coexistence of small populations with limited potentials for expansion is one of the main factors permitting the high species diversity of the tropical microhabitats.

In the antarctic ecosystems, on the contrary, the soil arthropod populations show enormous fluctuations of density, "pulsating" from extremely high aggregations to a dispersion of individuals, which can even lead to a random distribution (Di

Castri, 1969). They correspond in a most typical and extreme way to the conditions of the r-selection type, while the populations of the tropics approach a K-selection strategy (Pianka, 1970). The mean density of soil-related arthropods during the antarctic summer was found to be 8667 individuals per dm^3 (Di Castri et al., 1970), that is, almost four times the density found in the hygrophilous forests of central Chile. However, mean densities are almost meaningless under such unstable conditions, since both the lowest and the highest records of density in the whole latitudinal gradient have been observed in Antarctica (for instance, densities of 116 764 and 93 674 arthropods per dm^3 in terrestrial algae and mosses, which have no equivalent levels in any of the South American samples).

The situation in the mediterranean sclerophyllous formations, as regards aggregation, is an intermediate one, but certainly closer to that in tropical forests than in the antarctic ecosystems. However, within the same region, great differences can be noticed. In the hygrophilous forests of the coastal mountains, the range of aggregation values rather approach those found in the tropics. In irrigated fields, on the other hand, there is a "pulsation" of the populations from strong aggregation to extreme dispersion, which is somewhat comparable to the "antarctic" pattern.

In Fig. 24.4 (presented in a very schematic way), diversity and density of soil arthropods are ex-
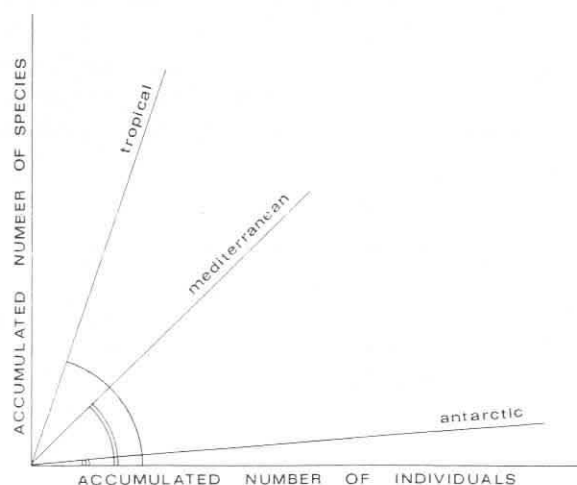

Fig. 24.4. Angles of species diversity of soil animals (determined by the lines of the accumulated number of individuals against the accumulated number of species) in tropical, mediterranean and antarctic areas (same regions as in Fig. 26.3).

pressed in an unusual (but simple) way, which can be defined as the "angle of species diversity". Given a scale starting at 1, if hypothetically all the individuals collected in a series of samples (from a site or from a gradient of sites) belong to the same species, the angle would be 0°; if each new individual corresponds to a new different species, the angle would be 90°. The antarctic situation, with a small angle, approaches the first type (and in fact mono-specific samples have sometimes been collected in Antarctica); the tropical situation, with a large angle, tends towards the second type (but it is a biological impossibility that 90° be reached). The mediterranean situation (represented here by the sclerophyllous formations) is again intermediate, and oscillates towards the tropical pattern in complex and dense plant formations (hygrophilous forests) or towards the antarctic pattern in more open (semi-deserts) and particularly in man-disturbed (irrigated fields) ecosystems.

As regards the stratification of species diversity (Fig. 24.5), the extreme case is represented by the antarctic soil fauna, since the very skeletal soils prevent a penetration in depth. In the mediterranean ecosystems, as already explained in the introduction of this chapter, the selective forces (seasonal drought, permeable soils with good aeration) induce a colonization towards the depth, thus increasing the underground stratification and the concavity (or "thickness") of the ecosystem (see Di Castri, Chapter 1). This trend applies to both the soil fauna and the soil microflora; relatively important populations of soil animals and microbes have been found in Chile and in the Mediterranean Basin at almost 1 m depth, and even more along the roots

Fig. 24.5. Patterns of stratification of soil arthropods in tropical, mediterranean and antarctic areas (same regions as in Fig. 26.3). Species diversity of soil arthropods (in bits per individual) calculated according to Shannon's formula.

which penetrate into the interstices of fractured rocks.

In wet tropical ecosystems, on the contrary, the selective forces (air saturated with moisture under the tree canopy, strong development of epiphytes, soils nutrient-poor at depth and frequently with excess of water and anoxia phenomena) impel the hygrophilous and aerobic soil-related animals to colonize the upper microhabitats (along the trunks, on the branches, in the "epiphytic soils"), thus increasing their above-ground stratification and therefore the "biological convexity" of the ecosystem. The maximum of species diversity is in the most superficial litter layer, where there exists also a very dense rootlet mat (and where most of the biochemical processes of nutrient cycling take place), decreasing very sharply towards the deeper horizons. Ecological conditions somewhat similar to the tropical ones as regards stratification of the soil fauna are found in the hygrophilous temperate and cold forests of the Valdivian and Magellanic regions of Chile, and even in mediterranean-climate areas in the coastal "fog" forests.

RELATIONSHIPS OF SOIL WITH OTHER MICROHABITATS

Soil is by no means a closed system, not only because of the cycling of nutrients and the exchange of energy and information with the above-ground subsystem (Di Castri et al., 1965a), but also because soil-related organisms have a potential of colonizing several other habitats; conversely, many organisms inhabiting different habitats search for the soil environment during a part of the year or a part of their life cycle as a refuge from climatic instability. A sort of habitat turnover is established, therefore, between the soil and the neighboring environments, with a daily or seasonal periodicity.

This section has a two-fold objective: firstly, to highlight the evolutionary potentials of several soil animals to expand their distribution by colonizing very diverse terrestrial environments; and secondly, from a methodological viewpoint, to stress again that this ecological research should not be focused exclusively on a very restricted biotope and at the site level; a lack of appreciation of the complexity of the interrelationships would then bias the conclusions, not only in ecological topics, but even
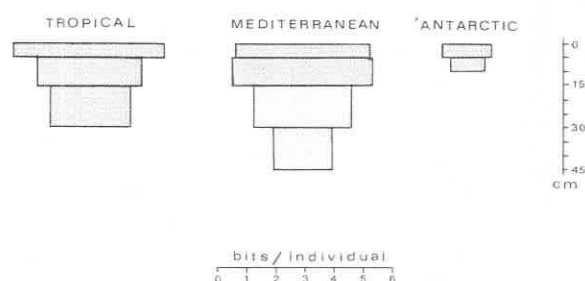
more in biogeographical and taxonomic aspects (immature specimens and adults often occupy a different microhabitat or soil stratum). While the previous section of this chapter has dealt with the variations along an extremely extended latitudinal gradient with replacement of ecosystem types, this section covers a scale of a few meters along which these different microhabitats are stepped.

The relations between the soil animals and the populations of decaying wood, rocks and trees have been discussed in general terms by Wallwork (1976). Travé (1963) paid particular attention to the distribution and ecology of the oribatid mites in several non-edaphic habitats, some of them situated in the mediterranean-climate zone of France.

Fig. 24.6 shows the affinity [or "similarity", expressed by Sørensen's (1948) quotient] at the species level between the arthropod communities inhabiting four superposed strata, from the deep soil up to mosses on a tree trunk, in a Chilean formation with a mediterranean humid climate. The moss community appears as a kind of "dependency" of the litter and the humus, since it shares a large number of species with the other two microhabitats.

The crossroad position of humus is clearly depicted in Fig. 24.6. Humus is at the same time the point of departure for the colonization of other environments, and a refuge for a fauna of different origins, thus constituting the "core" of the highest species diversity of both animals and microbes (and in general of the overall ecosystem). Humus is also a connecting link between the autotrophic, energy-storing vegetation and the microbial communities; the latter mineralize part of the organic matter and reorganize part of it as humified constituents, which can be considered as a source of stored information (Di Castri et al., 1965a; Schaefer, 1973). As the centre of biochemical information and of biological complexity, humus is also a key centre of regulation of the mediterranean ecosystem as a whole (Di Castri, 1966). Unfortunately, little is still known on the biochemical processes of humification and humus degradation under mediterranean climates and sclerophyllous vegetation, or on the characteristics of the organic matter of different mediterranean soils (for southern France, see Bottner, 1970). In addition several agricultural practices acting on such erosion-prone soils as the mediterranean ones, cause a sort of "decapitation" of the
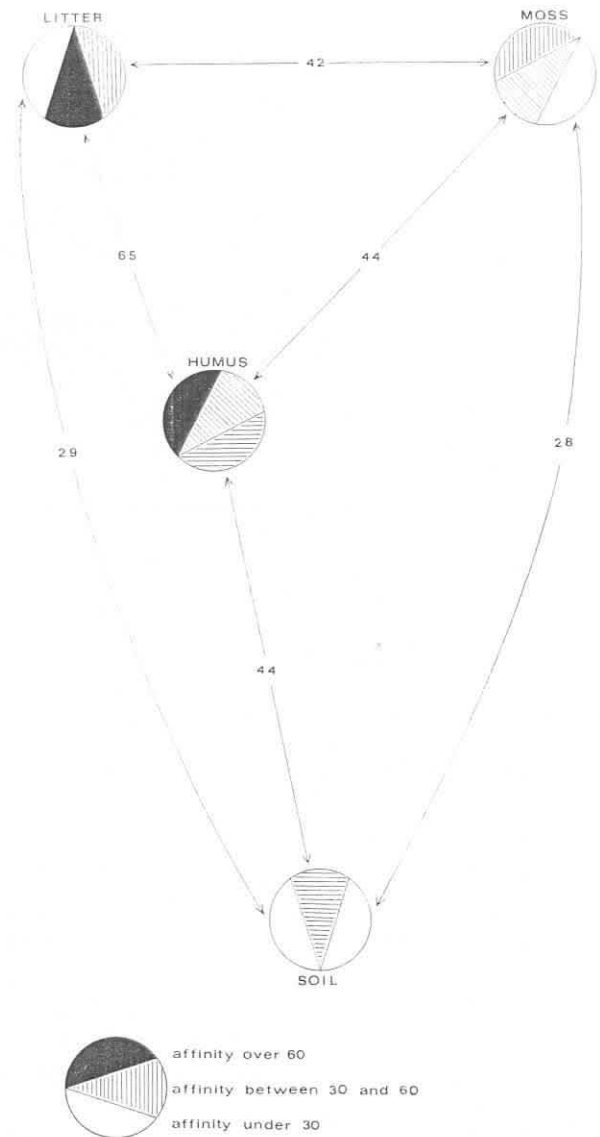
Fig. 24.6. Species affinities (according to Sørensen's quotient) between arthropod communities inhabiting the deep soil, the humus layer, the litter and the mosses on trees, in Chile.

humus layer from the soil profile (Di Castri, 1966); some of the detrimental biological effects discussed earlier in this chapter are explained by the extreme humus impoverishment of these soils.

A series of microhabitats colonized by humicolous and edaphic (soil-related) species of animals is schematically shown in Fig. 24.7. Two preliminary observations should be made as regards this figure. Firstly, the trend of the migrations can be both upward and downward. Secondly, for some

Fig. 24.7. Microhabitats inhabited by soil-related species of invertebrates in environmental gradients controlled by increased aridity (left side) and increased moisture (right side).

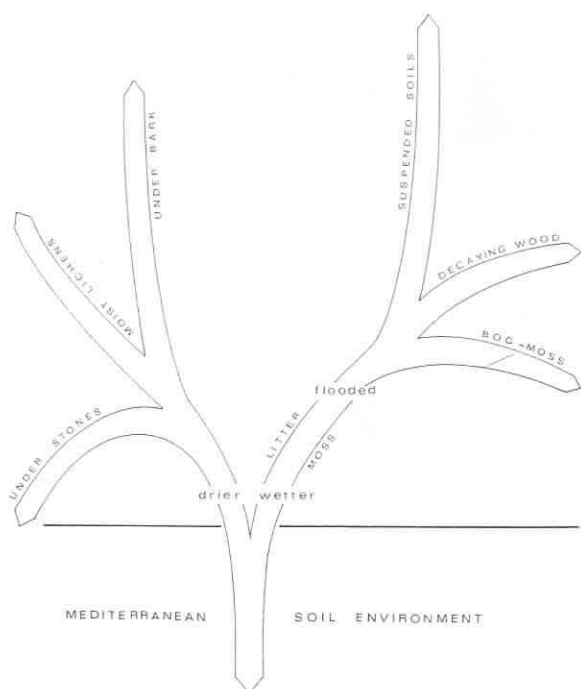species it may represent their present-day habitat turnover in a given site; for some groups of phylogenetically related species, the latitudinal shift of the stratum occupied by them; for other species, finally, the sense of their evolutionary history which had linked them irreversibly to a very specialized microhabitat; it depends on the degree of evolutionary plasticity or specialization that a given species has reached.

With this different time perspective in mind, one can draw the general conclusion that animal species search (or have searched) for the soil environment when they have to escape conditions of a strong climatic seasonality (summer drought, too cold winters). Conversely, they leave (or have left) the soil when it becomes too dry (even at depth), or anoxic due to waterlogging and water saturation of the soil interstices. In a latitudinal ecosystem gradient, for instance, the first case would correspond to semi-deserts and deserts, the second to some tropical savannas and forests on flat lands and to the moorlands. With increasing aridity in geological or present-day ecological terms (see Fig. 24.7), animals find refuge under stones (where even in

deserts some moisture remains because of the dew or occasional rainfall), in lichens on rocks and plants (or other epiphytes like *Phrygilanthus aphyllus*, "quintral" in Chile, which grows on Cactaceae such as *Trichocereus* and *Eulychnia*) which can intercept and concentrate the atmospheric moisture, or under the bark of deep phreatophytes having water-trapping devices in bark and branches. With increasing waterlogging and flooding (Fig. 24.7), these hygrophilous (but strictly aerobic) animals can find refuge in upper environments, including the fronds of ferns, if air is almost saturated with moisture.

Finally, Fig. 24.8 illustrates the occupation by soil arthropods of new microhabitats in a man-modified environment (cultivated and irrigated fields in the central zone of Chile). Taking as a benchmark the soil communities isolated in a deep hole of an old tree of *Acacia caven*, which represents
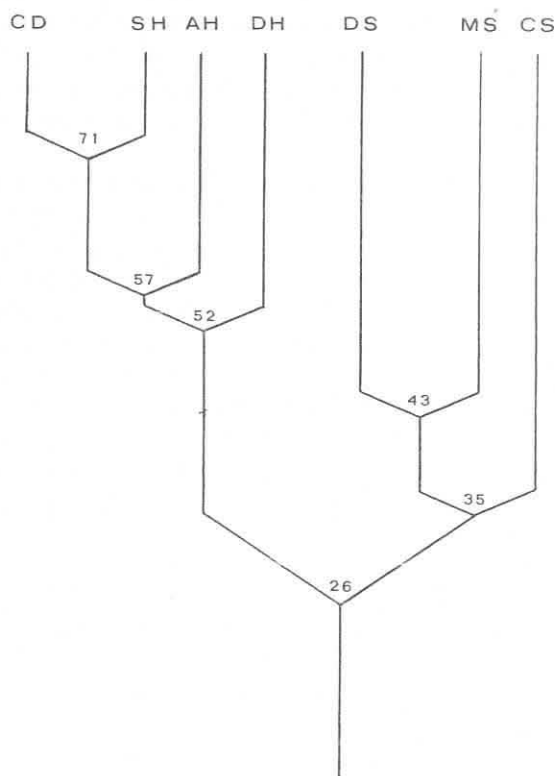

Fig. 24.8. Dendogram of species affinities (according to Sørensen's quotient) between microhabitats of a cultivated field in the mediterranean-climate zone of Chile (from Di Castri and Covarrubias, 1965). *CD* = cow dung; *SH* = superficial soil horizon; *AH* = *Acacia caven* tree hole; *DH* = deep soil horizon; *DS* = decaying trench silo; *MS* = maize silo; *CS* = clover silo.

the relatively most natural situation, it becomes evident that, together with specialized elements, there still exists in these communities a plastic component able to colonize such unstable and recent microhabitats as cow dung and even trench silos.

BIOGEOGRAPHICAL ROOTS OF ADAPTATION OF SOIL ANIMALS

In the introduction of this chapter, the fact was mentioned that, in the mediterranean-climate regions, different groups and species of soil animals show a multiplicity of evolutionary strategies and of mechanisms of adaptation to the peculiar environmental feature of these regions, that is, the extended summer drought. Furthermore, Di Castri (Chapter 1) has referred to the variety of elements from different biogeographical origins which exist in the communities of mediterranean-climate soils. The coexistence of so many life forms and of species with such different geological histories is possible because of the temporal and spatial heterogeneity of the mediterranean lands (Di Castri, Chapter 1). An additional scale of heterogeneity exists in relation to the soil communities, where there are gradients of microscopic habitats defined by extremely small microclimatic, microstructural and biochemical variations, due to different types of leaf litter and of humus, differences in the salt content of the soil, differences in soil particles, soil micro-agglomerations and intergranular spaces (for these micropedological aspects, see the classical work of Kubiëna, 1938).

In this chapter, **morphological** adaptations leading to life forms such as the soil "water" animals or the eu-edaphic (strictly soil-living and aerobic animals) species, **physiological** adaptations such as aestivation in a state resembling anhydrobiosis, **developmental** adaptations such as neoteny (the adults conserving some of the larval characteristics, e.g., smaller size and apterism, because of a delay or limitation in the post-embryonic development), **behavioral** adaptations such as vertical migrations in soil or habitat turnover, have been frequently discussed. Therefore, the aim of this section is not to cover comprehensively the different ways of adaptation, but only to present more systematically some of the evolutionary strategies which have been described earlier in this chapter.

The first category of evolutionary strategies refers to the mechanisms of **escape** (Di Castri, 1973c) or **avoidance** (Wallwork, 1976) *vis-à-vis* the prevailing climatic conditions. Three main forms of avoidance can be recognized in relation to the mediterranean climate: life at depth where the soil horizon maintains favorable conditions of moisture all through the year (**eu-edaphism**); life in a state of dormancy or diapause during the dry period (**aestivation**); **migrations** within the soil profile or **habitat turnover** with the neighboring microhabitats.

Among the animals living at depth, some of them (such as the Protura and several groups of Collembola) seem to be **primarily adapted** to the soil environment, since there are no related taxa living at the surface. In the few cases when these groups can be found in other microhabitats (such as mosses or suspended soils), the moisture saturation of the air is such as to resemble that in the deep soil.

On the other hand, other groups have close relatives (at the level of tribe or genus) living permanently in the epigeous (ground surface) environment. They are, therefore, **secondarily adapted** to live in deep soil, and show progressive degrees of morphological adaptations (apterism, depigmentation, small size and filiform body) according to the strictness of their life at depth and/or to the geological time at which the phylogenetic line began to search for refuge in the soil environment. This evolutionary strategy applies mostly to the endogeous beetles (Coleoptera), particularly to the families Staphylinidae, Pselaphidae, Scydmaenidae, Ptiliidae (= Trichopterygidae), Curculionidae, Colydiidae, and Carabidae. For some of the endogeous beetles, such as the Leptotyphlinae (Staphylinidae) and the genus *Mayetia* (Pselaphidae), the adaptation to life at depth is so integral or so ancient that they now lack close ties with epigeous forms. The evolution and ecology of soil beetles are treated comprehensively in two monographs of Coiffait (1958, 1959), while Jeannel (1965) refers in general to the origins of soil colonization by these arthropods, and Sáiz (1973) discusses in particular some biogeographical aspects of soil beetles in the mediterranean-climate regions.

Another mechanism of avoidance is of a passive nature; it consists in passing through the unfavorable period (dry season) in a dormancy-like state; since the unfavorable period under mediterranean climates corresponds chiefly to the summer, this

adaptation is called aestivation. Aestivation has already been discussed in some detail in this chapter. It can be performed by adults in a state resembling anhydrobiosis (e.g., some Collembola such as *Folsomides*) or in the anabiosis of some Mollusca (Di Castri, 1973c; Wallwork, 1976), by means of resistant eggs (e.g., some Collembola such as *Sphaeridia*), by means of cysts as in most of the soil "water" animals, or by spores as in many soil bacteria and fungi.

The last mechanism of avoidance is an active one; through migrations within the soil profile or towards other microhabitats, several groups of animal escape periodically from the unfavorable conditions, searching for those more suited to their ecological tolerance. Their migrations can be occasional (in response to changes in the soil moisture) or cyclic in nature; cycles can be of a 24-h periodicity, seasonal, or corresponding to ontogenic development (usually *larvae* living in soil, and adults in the upper environment, as in many insects).

The second category of evolutionary strategies of soil animals involves specific adaptations to the summer drought of the mediterranean climate, through physiological or behavioral means. These can be called mechanisms of **tolerance** (Wallwork, 1976). Among the mechanisms for reducing water loss (i.e., to lower the basic transpiration) are the strong and almost impermeable cuticles of several Tenebrionidae beetles. Mention has already been made of the excretory adaptations of some South Australian Megascolecidae, which also favor water conservation in summer (Jamieson, 1974). The ability of certain species of woodlice (Isopoda) and of pill millipedes (*Glomeris*) to conglobate also allows these animals to lose considerably less water, according to Warburg (1965, 1968). It has also been suggested that some desert invertebrates have the possibility of active uptake of water from unsaturated air (Edney, 1967). For a first comprehensive discussion of the water relations of terrestrial arthropods, reference should be made to the monograph of Edney (1957).

It is important to draw attention to the relativity of these concepts, both of the mechanisms of avoidance and of tolerance; there are no sharp divisions among them, but transitional processes and strategies. For instance, research on experimental gradients of soil moisture, established by con-

trolled irrigation and carried out in central Chile by the authors and their co-workers, has demonstrated that some edaphic invertebrates such as the Protura can shift their living stratum upwards in the soil profile. Similarly, some "endogeous" beetles are found in the superficial humus layers in rainier areas with a mediterranean perhumid climate. For some taxa of Crustacea, there is even a transition between aquatic and terrestrial life, as shown by Löffler (1966) for the copepods and by Edney (1968) for the isopods.

In addition, the fundamental question to clarify is whether or not (and to what extent) these evolutionary strategies and these mechanisms of adaptation are peculiar to the mediterranean-climate soils, or can be found elsewhere. The unequivocal reply to that question is that most of these strategies **are not** typical of the mediterranean environment. The "tolerance" adaptations are all referable to a desert environment (Wallwork, 1976). Most of the adaptations embraced under the term of "aestivation" (anabiosis, resistant eggs, encystment, sporulation) can also occur in the other ecosystem types (e.g., deserts, tropical savannas, mountain and tundra ecosystems) when the prevailing climatic conditions become unfavorable (while not necessarily, or not primarily, in the summer). In Australia, for instance, the "aestivation" of Collembola (*Folsomides*) has been observed in desertic (Wood, 1971) as well as in mediterranean-climate soils (Greenslade, 1974, 1975).

If the habitat turnover of soil animals and life at depth are far from being unique to the mediterranean environment, they are, nevertheless, the evolutionary strategies which at least seem to be more frequent in the mediterranean communities than in other ecosystems. Habitat turnover, including changes of strata within the soil profile, exists in all ecosystems, but in the mediterranean regions is facilitated by their great spatial and temporal heterogeneity (Di Castri, Chapter 1). Life of aerobic arthropods at depth is also common in other temperate-climate ecosystems (particularly deciduous and mixed forests, and some grasslands), and even in the tropics in some mountainous areas. However, deep soil profiles on gentle slopes, with good aeration and without waterlogging (except some occasional flooding in the winter), associated at present with dry seasonal conditions at surface, but preserved by the massive glaciations of the

Quaternary (that is, all the prerequisites for the eu-edaphic life), occur predominantly in some mediterranean-climate areas.

In conclusion, if most of these adaptations do not depend primarily on the existence of the present-day mediterranean climate, it is because they had been acquired by the soil fauna long before the appearance of that climate (see also Di Castri, Chapter 1). Some of them are related rather to humid and subhumid conditions (either temperate or tropical), others to desertic conditions. Research on the adaptive mechanisms of the soil fauna under mediterranean climates cannot be dissociated, therefore, from a profound knowledge of the biogeographical origin of the group under study; they depend on the geological history of that group at least as much as on present-day climatic conditions. This is what is meant by the title of this section — the "biogeographical roots of the adaptation of soil animals".

This point stresses again the danger of generalizing when only one site (or a few sites) and/or only one taxonomic group (or a few taxa) are taken into consideration. For instance in Chile, if mostly hygrophilous taxa were to be considered (e.g., some of the Collembola, the endogeous beetles, the numerous species of Pseudoscorpionida *Austrochthonius* or Gymnobisiidae), it might be concluded that the mediterranean zone of Chile is the northernmost end of a continuum of temperate communities of Valdivian and Magellanic origin (or of Paleoantarctic origin in a more ancient geological time dimension). If, on the other hand, xerophilous groups of Tenebrionidae, Pseudoscorpionida Olpiidae and some of the Arachnida were under consideration, one might argue that the mediterranean zone of Chile represents the southernmost end of a continuum of desertic and arid Andean formations. The situation would be different in South Africa and southern Australia, since these regions now lack continuity with areas with temperate humid climates (though their soil communities retain a number of "temperate" elements of Paleoantarctic origin), while they present a continuous range with subtropical and tropical ecosystems; in fact, in relation to plants, Specht (1980) demonstrated that the understory of the mallee communities with a mediterranean arid climate in southern Australia is "the southernmost end of a continuum of diverse plant communities

from subtropical coastal Queensland". It is not surprising that, in the recent book of Wallwork (1976) on the distribution of soil fauna, the "mediterranean" animals are treated sometimes in the chapter on hot deserts, sometimes in relation to grasslands or to temperate and subtropical forests.

In synthesis, the peculiar feature, the "intrinsic" nature of mediterranean biogeography, at least as regards the soil animals, is not the presence of given phylogenetic lines or the occurrence of a given evolutionary strategy, but the superposition of remnants of successive geological eras and the coexistence of the most diverse evolutionary strategies, due both to the conservative capability and the heterogeneous characteristics of the lands with a present-day mediterranean climate (see Ch. 1).

In addition to having accumulated derivatives from tropical, temperate and desertic faunas, during the Pleistocene these lands acquired the mediterranean climate with several localized subclimates. With the concomitant large changes in topography (new orographic features, physiographical fragmentation of small isolated territories, exposure of new rocks and formation of new soils), this change accelerated the speciation of soil invertebrates to such an unprecedented rate that the term "pulverization" (Di Castri, 1973c) has been used to designate the micro-scale segregation of phylogenetic lines, giving rise to innumerable species of an extremely restricted distribution; this segregation was even more marked for the arthropods which remained as "refugees" in the deep soil, with very limited ability for dispersion.

Given the enormous variability of biogeographical patterns in the five mediterranean-climate regions for the different groups and species of soil animals, any global generalization would be, almost by definition, an oversimplification. World maps of distribution of some "mediterranean" animals have been prepared by Sáiz (1973) and Vitali-di Castri (1973). To illustrate in this chapter some biogeographical affinities among the five regions, the faunas of pseudoscorpions will be taken as an example, for the following reasons:

(a) It is a group particularly well represented in the sclerophyllous formations with a mediterranean climate, not only in the soil, but also in the related microhabitats (under bark, under stones, in litter and moss).

(b) It is a group which comprises hygrophilous

(like most of the Chthoniidae), mesophilous (like several Chernetidae), and xerophilous (e.g. Olpiidae) species.

(c) Its taxonomy is relatively well known in the five regions with a mediterranean climate (Vitali-di Castri, 1973).

(d) Lines of very different geological history are recognizable. For instance, Vitali-di Castri (1973) described for the fauna of mediterranean Chile ten major components: three very ancient probably Gondwanan lines, one of them with a very fragmentary relict distribution in some regions with a mediterranean climate (the Menthidae in California, Israel and Chile, see Vitali-di Castri, 1969c), a second (e.g. Cheiridiidae) with a pantropical distribution, and a third (e.g. Olpiidae) widely distributed in all the desertic zones of the world; three Paleoantarctic hygrophilous lines which demonstrate, through their varying patterns of distribution in the austral continents, different times of geological separation from a very ancient Cretaceous origin to a Tertiary derivation (see also Di Castri, Chapter 1, Fig. 1.8); neotropical species;

elements of amphitropical (Chile – western North America) distribution, having probably migrated along the Andes; "mediterranean" endemics; and cosmopolitan species carried by man. Mechanisms such as neoteny in the Cheiridiidae (Vitali-di Castri, 1966) and sexual dimorphism in the Gymnobisiidae (Vitali-di Castri and Di Castri, 1970) would have further promoted speciation in the mediterranean-climate areas.

(e) Finally, the pseudoscorpions constitute a group fairly representative of the patterns of biogeographical distribution shown by several other taxa of soil animals.

Fig. 24.9 presents a world map with the affinities (at family and genus level) among the faunas of pseudoscorpions of the five regions with a mediterranean-type climate. Affinities have been calculated by means of the "simple matched coefficient", derived from methods of numerical taxonomy (Sokal and Michener, 1958; Sokal and Sneath, 1963). The lowest affinities are not shown in the figure. It should also be pointed out that inter-continental affinities at the species level have not

Fig. 24.9. Affinities (at family and genus level) among the Pseudoscorpionida faunas of the five regions of the world with a mediterranean-type climate (modified from Vitali-di Castri, 1973). The degree of affinity is directly proportional to the thickness of lines.

been calculated, since almost no common species exist among these regional faunas, with the exception of a few cosmopolitan ones.

Three main conclusions can be advanced from the analysis of Fig. 24.9:

(1) The level of affinity among these soil faunas is much higher than that which a similar analysis of the dominant mediterranean shrubs would have shown, at least as regards the three regions of the Southern Hemisphere (in fact, there are almost no genera of overstory plants in common). The weight of a common, very ancient geological heritage is, therefore, more marked for the soil fauna than in the case of most of the vegetation and of the vertebrates.

(2) Affinities are greater in a transverse (east–west) than in a north–south direction, in spite of the present-day territorial continuity between South and North America, and between South Africa and the Mediterranean Basin (and in spite of the present-day large separation by the oceans of the other regions). These old phylogenetic linkages are attributable to the existence in the Cretaceous of a northern Laurasian continent (embracing North America and Eurasia) and of the southern Paleoantarctic lands, connecting Antarctica, South America, Australia and part of South Africa (or with bridges with South Africa). For the sequence of geological events, attention is drawn to Fig. 1.8 (Di Castri, Chapter 1).

(3) "Vertical" affinities are greater between California and Chile (and also of a rather recent nature, being high at generic level), than between South Africa and the Mediterranean Basin, in spite of the fact that the connection between North and South America was re-established only at the end of the Tertiary through the Isthmus of Panama. Unlike the barrier represented by the Sahara Desert, the Andes, because of their north–south extension, acted as a kind of bridge facilitating the passage and migration of mesic and cold-tolerant species across the wet tropical forests of northern South America and the extremely dry Atacama Desert southward.

CONCLUSIONS

The soil animal communities of the five regions with a mediterranean climate have a number of structural patterns in common, which can mainly be ascribed to the deep stratification in the soil, migrations within the soil profile, as well as to and from neighboring environments (habitat turnover), and the phenological behavior with a minimum of activity and of density during the summer. Physiological (e.g. aestivation) and morphological (e.g. strong chitinization of ground animals, "euedaphic" adaptations of deep soil animals) convergences exist also between comparable animal groups of the five regions; some of these convergences, however, are attributable to adaptations acquired before the appearance of the mediterranean climate, under desert, temperate (humid and cool to cold) or tropical conditions. In addition to having accumulated derivatives from different climatic periods and diverse biogeographical origins the "mediterranean" lands were the center of an unprecedented phenomenon of accelerated speciation during the Pleistocene, because of the appearance of the mediterranean climate and of the concomitant large-scale orogenic and topographic changes which took place in most of these regions. This helps to explain the high species diversity shown by several soil animal communities of the mediterranean zones.

There are more phylogenetic affinities between the soil faunas of the five mediterranean-climate regions than in their vegetation. Furthermore, the influence of their historical and geological heritage on soil communities appears to be more pervasive than that of the present-day climatic conditions.

Considering the great spatial and temporal heterogeneity of the mediterranean lands and ecosystems, the restricted distribution of the soil animals and of the soil communities, as well as their close dependence on historical factors, make them excellent ecological indicators of soil characteristics (including the origin of the soil and pedogenetic processes) and good biogeographical indicators of the degree of similarity between different disjunct ecosystems, as well as possible benchmarks for evaluating the degree of man's impact (both duration and intensity) on given soils.

The **gradient approach** (an environmental gradient taken as unit for research) is the methodological response to the heterogeneity of the mediterranean environment (Di Castri, 1973b). In this chapter, in addition to the intercontinental comparisons among the five regions, results have been

presented regarding **latitudinal** gradients, **topographical** gradients (which, including the valley bottom and the two pole-facing and equator-facing slopes, can represent a microcosm of almost all latitudinal conditions), **altitudinal** gradients (to a certain extent, a recapitulation of the polewards latitudinal gradient), **habitat** gradients controlled by the varying availability of moisture or the level of soil nutrients, **microhabitat** gradients (from the "arboreal" soil-related fauna to the "deep soil" fauna; microstructural, microclimatic and biochemical gradients in the soil), **anthropogenic** gradients (as regards the number of years of man's manipulation and/or the intensity of man's impact), and **experimental** gradients (experimental burning, varying degrees of inundation through controlled irrigation, removing or interchanging of different types of litter, etc.).

As the nucleus of the highest species and biochemical diversity, humus represents the centre of regulation of the soil subsystem and, to a certain extent, of the whole ecosystem. The patterns of distribution of soil animals, their aggregation and relative abundance, as well as the physical conditions of their habitat ("filtering" of atmospheric stresses, potential for water absorption and retention, pore spaces and interstices), are largely determined by the humus characteristics, which, on the other hand, depend ultimately on the activities of soil organisms. However, little is known about humification processes under a mediterranean climate in a litter formed mostly of coriaceous leaves, rich in secondary plant-chemical compounds; even less is known about the conditions of humification under different agricultural and forestry practices. In more general terms, very important gaps still exist in knowledge of the rôle of soil nutrients and of soil organisms as determinants of the structure and the functioning of the mediterranean-type ecosystem as a whole.

REFERENCES

Alicata, P., Arcidiacono, R., Caruso, D. and Marcellino, I., 1972. Distribuzione dei microartropodi del suolo della lecceta di Castelporziano (Roma). *Boll. Sedute Accad. Gioenia Sci. Nat. Catania*, 11: 3–11.

Alicata, P., Arcidiacono, R., Caruso, D. and Marcellino, I., 1973. Distribution et fluctuations saisonnières des populations de quelques espèces d'Oribatides (Acariens) du sol d'un bois de chênes verts de l'Etna. *Rev. Ecol. Biol. Sol*, 10: 535–557.

Armesto, J.J. and Gutierrez, J.R., 1978. El efecto del fuego en la estructura de la vegetación de Chile Central. *An. Mus. Hist. Nat., Valparaiso*, 11: 43–48.

Armesto, J.J. and Martinez, J., 1978. Relations between vegetation structure and slope aspect in the mediterranean region of Chile. *J. Ecol.*, 66: 881–889.

Astudillo, V., Morales, M.A. and Loyola, R., 1966. Problemas en el análisis estadístico de poblaciones con distribución contagiosa. In: *Progresos en Biología del Suelo. Actas del Primer Coloquio Latinoamericano de Biología del Suelo*. Monografías I, UNESCO, Montivideo, pp. 359–369.

Athias-Henriot, C., 1969. Gamasides chiliens (Acariens Anactinotriches). 1 — Genre *Anephiasca* n. g. (Ascidae). *Rev. Biol.*, 7: 123–149.

Axelrod, D.I., 1973. History of the mediterranean ecosystem in California. In: F. di Castri and H.A. Mooney (Editors), *Mediterranean Type Ecosystems, Origin and Structure*. Ecological Studies, Analysis and Synthesis, 7. Springer-Verlag, Berlin, pp. 225–277.

Badonnel, A., 1963. Psocoptères terricoles, lapidicoles et corticicoles du Chili. In: C. Delamare Deboutteville and E. Rapoport (Editors), *Biologie de l'Amérique Australe, 2*. Centre National de la Recherche Scientifique (C.N.R.S.), Paris, pp. 291–338..

Badonnel, A., 1967. Psocoptères édaphiques du Chili (2e note). In: C. Delamare Deboutteville and E. Rapoport (Editors), *Biologie de l'Amérique Australe, 3*. Centre National de la Recherche Scientifique (C.N.R.S.), Paris, pp. 541–585.

Badonnel, A., 1971. Psocoptères édaphiques du Chili (3e note). *Bull. Mus. Hist. Nat., Paris, 3e Sér., Zool.*, 1: 1–38.

Bahre, C.J., 1979. *Destruction of the Natural Vegetation of North-Central Chile*. Univ. Calif., Publ. Geogr., 23: 117 pp.

Balogh, J., 1958. *Lebensgemeinschaften der Landtiere*. Akademie-Verlag, Berlin and Akadémiai Kiadó, Budapest, 560 pp.

Bamforth, S.S., 1971. The numbers and proportions of Testacea and Ciliates in litters and soils. *J. Protozool.*, 18: 24–28.

Bigot, L. and Bodot, P., 1972. Contribution à l'étude biocoenotique de la garrigue à *Quercus coccifera*: étude descriptive de l'habitat et de la faune des Invertébrés inventoriés. *Vie Milieu*, 23: 15–43.

Bigot, L., Grauby, A., Poinsot, N., Rougon, C., Rougon, D. and Tchernia, F., 1973. Influence d'une irradiation gamma chronique sur la faune et la microflore d'un écosystème forestier à Cadarache. *Radioprotection*, 8: 243–256.

Billès, G., Cortez, J. and Lossaint, P., 1975. Étude comparative de l'activité biologique des sols sous peuplements arbustifs et herbacés de la garrigue méditerranéenne. I. — Minéralisation du carbone et de l'azote. *Rev. Ecol. Biol. Sol*, 12: 115–139.

Bonnet, L., 1959. Quelques aspects des populations thécamoebiennes endogées. *Bull. Soc. Hist. Nat. Toulouse*, 94: 414–428.

Bonnet, L., 1964. Le peuplement thécamoebien des sols. *Rev. Ecol. Biol. Sol*, 1: 123–408.

Bonnet, L., 1966. Le peuplement thécamoebien de quelques sols du Chili (1). *Protistologica*, 2: 113–139.

Bonniard de Saludo, P., 1969. Nouveaux Carabiques du Chili. *Bull. Soc. Hist. Nat. Toulouse*, 105: 311–328.

Bottner, P., 1970. La matière organique des principaux types de sols sous l'étage bioclimatique du chêne vert dans le Midi de la France. *Sci. Sol*, 1: 3–18.

Bottner, P., Grandjouan, G. and Nedelka, E., 1975. Classification des sols par une méthode multivariable. Application à une séquence bioclimatique méditerranéo-alpine sur roches-mères calcaires. *Geoderma*, 14: 15–46.

Bouché, M.B., 1969. L'échantillonnage des peuplements d'Oligochètes terricoles. In: M. Lamotte and F. Bourlière (Editors), *Problèmes d'écologie: L'échantillonnage des peuplements animaux des milieus terrestres*. Masson, Paris, pp. 273–287.

Bouché, M.B., 1975. Fonctions des lombriciens. III. — Premières estimations quantitatives des stations françaises du P.B.I. *Rev. Ecol. Biol. Sol*, 12: 25–44.

Cancela da Fonseca, J.-P., 1969. L'outil statistique en biologie du sol. VI. — Théorie de l'information et diversité spécifique. *Rev. Ecol. Biol. Sol*, 6: 533–555.

Cancela da Fonseca, J.P. and Vannier, G., 1969. Echantillonnage des microarthropodes du sol. In: M. Lamotte and F. Bourlière (Editors). *Problèmes d'écologie: L'échantillonnage des peuplements animaux des milieux terrestres*. Masson, Paris, pp. 207–236.

Cassagnau, P., 1961. *Ecologie du sol dans les Pyrénées centrales. Les biocénoses des Collemboles*. Hermann, Paris, 235 pp.

Cody, M.L. and Mooney, H.A., 1978. Convergence versus non-convergence in mediterranean-climate ecosystems. *Annu. Rev. Ecol. Syst.*, 9: 265–321.

Coiffait, H., 1958. *Les Coléoptères du Sol*. Suppl. No 7 à *Vie et Milieu*. Hermann, Paris, 204 pp.

Coiffait, H., 1959. Monographie des Leptotyphlites (Col. Staphylinidae). *Rev. Fr. Entomol.*, 26: 237–437.

Coiffait, H., 1962. Les Leptotyphlitae (Col. Staphylinidae) de Californie. *Rev. Fr. Entomol.*, 29: 154–166.

Coiffait, H., 1963. Les Leptotyphlitae (Col. Staphylinidae) du Chili. Systématique et Biogégraphie de la sous-famille. In: C. Delamare Deboutteville and E. Rapoport (Editors), *Biologie de l'Amérique Australe, 2*. Centre National de la Recherche Scientifique (C.N.R.S.), Paris, pp. 371–383.

Coiffait, H., 1964. Un nouveau Leptotyphlite de l'Afrique du Sud. *Rev. Fr. Entomol.*, 31: 13–17.

Coiffait, H., 1970. Nouveaux Leptotyphlinae du Maroc, de la Péninsule Ibérique et des Baléares. *Rev. Ecol. Biol. Sol*, 7: 145–150.

Coiffait, H. and Sáiz, F., 1964. Les *Xantholininae* du Chili (Col. Staphylinidae). *Bull. Soc. Hist. Nat. Toulouse*, 99: 510–524.

Coiffait, H. and Sáiz, F., 1965. Nouveaux *Leptotyphlinae* (Col. Staphylinidae) du Chili. Seconde note. *Rev. Ecol. Biol. Sol*, 2: 129–136.

Coiffait, H. and Sáiz, F., 1966. Les *Quediini* du Chili (Col. Staphylinidae). *Ann. Soc. Entomol. Fr. (N.S.)*, 2: 385–414.

Coiffait, H. and Sáiz, F., 1967. Aleocharidae du Chili. I. — Tribus *Oligotini, Myllaenini, Bolitocharini* (Col. Staphylinoidea). *Bull. Soc. Hist. Nat. Toulouse*, 103: 51–98.

Coiffait, H. and Sáiz, F., 1968. Les Staphylinidae (*sensu lato*) du Chili. In: C. Delamare Deboutteville and E. Rapoport (Editors). *Biologie de l'Amérique Australe, 4*. Centre National de la Recherche Scientifique (C.N.R.S.). Paris, pp. 339–472.

Coineau, Y., 1974. Eléments pour une monographie morphologique, écologique et biologique des *Caeculidae* (Acariens). *Mém. Mus. Natl. Hist. Nat. Paris, Sér. A*, 71: 1–299.

Condé, B., 1974. Palpigrades du Chili. *Rev. Ecol. Biol. Sol*, 11: 449–455.

Cortez, J., Billès, G. and Lossaint, P., 1975. Étude comparative de l'activité biologique des sols sous peuplements arbustifs et herbacés de la garrigue méditerranéenne. II. — Activités enzymatiques. *Rev. Ecol. Biol. Sol*, 12: 141–156.

Couteaux, M.-M., 1975. Quelques aspects des relations entre les Thécamoebiens et les sols. *Rev. Ecol. Biol. Sol*, 12: 45–55.

Covarrubias, R., 1966. Observaciones cuantitativas sobre los Invertebrados terrestres antárticos y preantárticos. *Inst. Antárt. Chil., Publ.*, No. 9: 1–62.

Covarrubias, R., 1967. New Oribatids (Acarina) from Chile. *Opusc. Zool. Budapest*, 7: 89–116.

Covarrubias, R., 1968. Observations sur la Genre *Pheroliodes*. I — *Pheroliodes roblensis* n. sp. *Acarologia*, 10: 657–695.

Covarrubias, R., Rubio, I. and Di Castri, F., 1964. *Observaciones ecológico-cuantitativas sobre la fauna edáfica de zonas semi-áridas del Norte de Chile (Provincias de Coquimbo y Aconcagua)*. Monografias sobre Ecologia y Biogeografia de Chile, 2. Universidad de Chile, Santiago, 109 pp.

Covarrubias, R., Rubio, I. and Di Castri, F., 1965. Densidad edáfica en comunidades naturales e intervenidas del Norte Chico de Chile. *Invest. Zool. Chil.*, Número especial Tercer Congreso Latinoamericano de Zoologia: 19–23.

Dajoz, R., 1967. Contribution à l'étude des Coléoptères Lathridiidae du Chili. In: C. Delamare Deboutteville and E. Rapoport (Editors), *Biologie de l'Amérique Australe, 3*. Centre National de la Recherche Scientifique (C.N.R.S.), Paris, pp. 587–609.

Debauche, H.R., 1962. The structural analysis of animal communities of the soil. In: P.W. Murphy (Editor), *Progress in Soil Zoology*. Butterworths, London, pp. 10–15.

Delamare Deboutteville, C., 1951. *Microfaune du sol des pays tempérés et tropicaux*. Suppl. No. 1 à *Vie et Milieu*. Hermann, Paris, 360 pp.

Den Heyer, J. and Ryke, P.A.J., 1966. A mesofaunal investigation of the soil in a thorn-tree (*Acacia karroo*) biotope. *Rev. Biol.*, 5: 309–364.

Di Castri, F., 1960. Prime osservazioni sulla fauna del suolo di una regione delle Prealpi Venete (Monte Spitz, Recoaro). *Atti Ist. Veneto Sci., Lett. Arti*, 118: 475–493.

Di Castri, F., 1963a. Significado biológico y económico de la fauna del suelo. *Bol. Univ. Chile*, No. 37: 25–31.

Di Castri, F., 1963b. Etat de nos connaissances sur les biocoenoses édaphiques du Chili. In: J. Doeksen and J. van der Drift (Editors), *Soil Organisms*. North-Holland, Amsterdam, pp. 375–385.

Di Castri, F., 1963c. Estado biológico de los suelos naturales y cultivados de Chile Central. *Bol. Prod. Anim.*, 1: 101–112.

Di Castri, F., 1966. Consideraciones sobre el estado de disclimax en las zoocenosis edáficas. In: *Progresos en Biologia del Suelo. Actas del Primer Coloquio Latinoamericano de Biologia del Suelo*. Monografias I. UNESCO, Montevideo, pp. 333–341.

Di Castri, F., 1968. Interferencias del hombre en los sistemas edáficos. In: *Progressos em biodinámica e productividade do solo*. Universidade Federal de Santa Maria. Santa Maria, pp. 133–143.

Di Castri, F., 1969. Effects of climate and weather on the structure of soil arthropod communities. In: S.W. Tromp and W.H. Weihe (Editors), *Biometeorology*, 4. Swets and Zeitlinger, Amsterdam, pp. 47–48.

Di Castri, F., 1970. Les grands problèmes qui se posent aux écologistes pour l'étude des écosystèmes du sol. In: J. Phillipson (Editor), *Methods of Study in Soil Ecology, Proceedings of the Paris Symposium*. Ecology and Conservation 2. UNESCO, Paris, pp. 15–31.

Di Castri, F., 1973a. Introduction to Section IV: Soil systems in mediterranean climate regions. In: F. di Castri and H.A. Mooney (Editors), *Mediterranean Type Ecosystems, Origin and Structure*. Ecological Studies, Analysis and Synthesis, 7. Springer-Verlag, Berlin, pp. 169–170.

Di Castri, F., 1973b. Soil animals in latitudinal and topographical gradients of mediterranean ecosystems. In: F. di Castri and H.A. Mooney (Editors), *Mediterranean Type Ecosystems, Origin and Structure*. Ecological Studies, Analysis and Synthesis, 7. Springer-Verlag, Berlin, pp. 171–190.

Di Castri, F., 1973c. Introduction to Section VI: Animal biogeography and ecological niche. In: F. di Castri and H.A. Mooney (Editors), *Mediterranean Type Ecosystems, Origin and Structure*. Ecological Studies, Analysis and Synthesis, 7. Springer-Verlag, Berlin, pp. 279–283.

Di Castri, F. and Astudillo, V., 1965. Influencias climáticas, edáficas y estacionales en la densidad de la fauna del suelo. *Invest. Zool. Chil.*, Número especial Tercer Congreso Latinoamericano de Zoología: 41–45.

Di Castri, F. and Astudillo, V., 1966a. Revisión crítica de las aplicaciones de la teoria de la información en zoología del suelo. In: *Progresos en Biología del Suelo. Actas del Primer Coloquio Latinoamericano de Biología del Suelo*. Monografias I, UNESCO, Montevideo, pp. 313–331.

Di Castri, F. and Astudillo, V., 1966b. Análisis de algunas causas abióticas de variación en la densidad de la fauna del suelo. In: *Progresos en Biología del Suelo. Actas del Primer Coloquio Latinoamericano de Biología del Suelo*. Monografias I, UNESCO, Montevideo, pp. 371–377.

Di Castri, F. and Covarrubias, R., 1965. Diversidad biótica y afinidad de zoocenosis edáficas en terrenos intervenidos. *Invest. Zool. Chil.*, Número especial Tercer Congreso Latinoamericano de Zoología: 24–31.

Di Castri, F. and Mooney, H.A. (Editors). 1973. *Mediterranean Type Ecosystems, Origin and Structure*. Ecological Studies, Analysis and Synthesis, 7. Springer-Verlag, Berlin, 405 pp.

Di Castri, F. and Vitali-di Castri, V., 1971. Colonización por organismos edáficos de territorios desérticos sometidos a riego (Estancia Castilla, Provincia de Atacama, Chile). *Bol. Mus. Nac. Hist. Nat. Chile*, 32: 17–40.

Di Castri, F., Hermosilla, W., Sáiz, F. and Vitali-di Castri, V., 1961. Primeras prospecciones sobre la fauna edáfica chilena. *Bol. IV Conv. Méd. Vet. Santiago*, 4: 29–33.

Di Castri, F., Astudillo, V. and Sáiz, F., 1964. Aplicación de la teoría de la información al estudio de las biocenosis muscícolas. *Bol. Prod. Anim.*, 2: 153–171.

Di Castri, F., Astudillo, V. and Sáiz, F., 1965a. Aplicación de algunos conceptos cibernéticos al estudio de la estratificación de zoocenosis edáficas. *Invest. Zool. Chil.*, Número especial Tercer Congresso Latinoamericano de Zoología: 1–7.

Di Castri, F., Hermosilla, W., Covarrubias, R., Sáiz, F. and Astudillo, V., 1965b. Densidad y diversidad biótica de la mesofauna edáfica en estapas altoandinas del Norte Grande de Chile. *Invest. Zool. Chil.*, Número especial Tercer Congreso Latinoamericano de Zoología: 13–18.

Di Castri, F., Covarrubias, R. and Hajek, E.R., 1970. Soil ecosystems in subantarctic regions. In: *Ecology of the Subarctic Regions, Proceedings of the Helsinki Symposium*. Ecology and Conservation 1. UNESCO, Paris, pp. 207–222.

Dunn, P.H. and DeBano, L.F., 1977. Fire's effect on biological and chemical properties of chaparral soils. In: H.A. Mooney and C.E. Conrad (Editors), *Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems*. Forest Service, U.S. Department of Agriculture, Washington, D.C., pp. 75–84.

Edmonds, S.J. and Specht, M.M., 1980. Dark Island heathland, South Australia: faunal rhythms. In: R.L. Specht (Editor), *Heathlands and Related Shrublands, B. Analytical Studies*. Ecosystems of the World, 9B. Elsevier, Amsterdam, pp. 15–27.

Edney, E.B., 1957. *The Water Relations of Terrestrial Arthropods*. Cambridge Monographs in Experimental Biology, 5. Cambridge University Press, Cambridge, 109 pp.

Edney, E.B., 1967. Water balance in desert arthropods. *Science*, 156: 1059–1066.

Edney, E.B., 1968. Transition from water to land in isopod crustaceans. *Am. Zool.*, 8: 309–326.

FAO–UNESCO, 1970–1978. *Soil Map of the World. 1:5 000 000*. Volumes I to X. UNESCO, Paris.

Follmann, G., 1963. Nordchilenische Nebeloasen. *Umschau*, No. 4: 101–104.

Franz, G. and Medina, P., 1968. *Caracterización microbiológica de algunos suelos naturales y cultivados de diferentes regiones ecológicas de Chile*. Trabajo presentado al Segundo Congreso Latinoamericano de Biología del Suelo, Santa Maria, Brasil, Julio 1968. Universidad de Chile, Santiago, 7 pp.

Franz, H., 1964. Neue Caeculiden aus Afrika und Südamerika. *Verh. Zool. Bot. Ges. Wien*, 103–104: 82–93.

Franz, H., 1967. Zur Kenntnis der Scydmaenidenfauna von Lateinamerika. In: C. Delamare Deboutteville and E. Rapoport (Editors), *Biologie de l'Amérique Australe, 3*. Centre National de la Recherche Scientifique (C.N.R.S.), Paris, pp. 611–724.

Froehlich, C.C., 1967. A contribution to the zoogeography of neotropical land planarians. *Acta Zool. Lilloana*, 23: 153–162.

Gastó, J. and Contreras, D., 1979. Un caso de desertificación en el Norte de Chile. El ecosistema y su fitocenosis. *Bol. Téc. Fac. Agron., Univ. Chile*, No. 42: 1–99.

Ghabbour, S.I., 1979. Soil invertebrates. In: M.A. Ayyad and M. Kassas (Editors), *Analysis and Management of Mediterranean Desert Ecosystems, Proceedings of the International Workshop of Samdene Project (Alexandria, January 1979)*. Alexandria University, Alexandria, pp. 102–105.

Ghilarov, M.S., 1958. L'importance du sol dans l'origine et l'évolution des insectes. *Proc. Tenth Int. Congr. Entomol. (Montréal, 1956)*, 1: 443–451.

Ghilarov, M.S., 1964. Connection of insects with the soil in different climatic zones. *Pedobiologia*, 4: 310–315.

Ghilarov, M.S., 1965. Connection of insects with the soil in different climatic zones. *Proc. XII Int. Congr. Entomol. (London, 1964), Section 6:* 405.

González, R.H. and Smith, L.M., 1964. Japygidae of South America, 5: new species of Japygidae from Chile. *Proc. Biol. Soc. Wash.*, 77: 35–45.

Greenslade, P., 1974. Ecological and zoogeographical notes on Collembola of Kangaroo Island, South Australia. *Pedobiologia*, 14: 256–265.

Greenslade, P., 1975. The role of soil fauna of arid shrubland in South Australia. In: J. Vaněk (Editor), *Progress in Soil Zoology. Proceedings of the 5th International Colloquium on Soil Zoology held in Prague, September 1973.* W. Junk, The Hague and Academia, Prague, pp. 113–119.

Greenslade, P.J.M. and Greenslade, P., 1973. Epigaeic Collembola and their activity in a semi-arid locality in Southern Australia during summer. *Pedobiologia*, 13: 227–235.

Guillaumont, F., 1977. Sur la biologie et l'écologie des espèces du genre *Hemineura* Tetens en Provence occidentale (Psocoptères Elipsocidae). *Ecol. Mediterr.*, 3: 55–65.

Hermosilla, W., 1962. *Observaciones ecológico-cuantitativas sobre la fauna edáfica del Cerro "El Roble".* Thesis, Universidad de Chile, Santiago, 50 pp.

Hermosilla, W. and Murúa, R., 1966. Estudio ecológico-cuantitativo de la fauna hipogea en las dunas de Concón-Quintero. *Bol. Prod. Anim.*, 4: 69–102.

Hermosilla, W. and Rubio, I., 1976. Structure des populations de Collemboles Poduromorphes dans une colline de la Cordillère de la Côte chilienne. *Rev. Ecol. Biol. Sol*, 13: 477–489.

Hermosilla, W. and Rubio, I., 1977. Vertikalverbreitung von Collembola Poduromorpha im Bergmassiv "El Roble" (Küstenkordillere, Chile). *Pedobiologia*, 17: 226–232.

Hermosilla, W., Covarrubias, R. and Di Castri, F., 1967. Estudio comparativo sobre la estructura de zoocenosis edáficas en el trópico y en la Antártida. *Arch. Biol. Med. Exper.*, 4: 210.

Hunt, J.H., 1977. Ants. In: N.J.W. Thrower and D.E. Bradbury (Editors), *Chile-California Mediterranean Scrub Atlas. A Comparative Analysis.* Dowden, Hutchinson and Ross, Stroudsburg, Penn., pp. 195–198.

Jamieson, B.G.M., 1974. Earthworms (Oligochaeta: Megascolecidae) from South Australia. *Trans. R. Soc. S. Aust.*, 98: 79–109.

Jeannel, R., 1963. Les Psélaphides de la Paléantarctide occidentale. Supplément. In: C. Delamare Deboutteville and E. Rapoport (Editors), *Biologie de l'Amerique Australe, 2.* Centre National de la Recherche Scientifique (C.N.R.S.), Paris, pp. 351–369.

Jeannel, R., 1964. Sur quelques Psélaphides du Chili. *Rev. Fr. Entomol.*, 31: 5–12.

Jeannel, R., 1965. La genèse du peuplement des milieux souterrains. *Rev. Ecol. Biol. Sol*, 2: 1–22.

Kaszab, Z., 1969. The scientific results of the Hungarian soil zoological expeditions to South America. 17. Tenebrioniden aus Chile (Coleoptera). *Opusc. Zool. Budapest.* 9: 291–337.

Kraus, O., 1966. Solifugen aus Chile (Arach.). *Senkenbergiana Biol.*, 47: 181–184.

Kubiëna, W.L., 1938. *Micropedology.* Collegiate Press, Ames, Iowa, 243 pp.

Kühnelt, W., 1955. An introduction to the study of soil animals. In: D.K. McE. Kevan (Editor), *Soil Zoology.* Butterworths, London, pp. 3–22.

Kummerow, J., 1962. Quantitative Messungen des Nebelniederschlages im Walde von Fray-Jorge an der nordchilenischen Küste. *Naturwissenschaften*, 9: 203–204.

Lawrence, R.F., 1953. *The Biology of the Cryptic Fauna of Forests, with Special Reference to the Indigenous Forests of South Africa,* A.A. Balkema, Cape Town, Rotterdam, 408 pp.

Le Berre, J.R., 1969. Les méthodes de piégeage des invertébrés. A. — Généralités. In: M. Lamotte and F. Bourlière (Editors), *Problèmes d'écologie: L'échantillonnage des peuplements animaux des milieux terrestres.* Masson, Paris, pp. 55–64.

Lee, K.E. and Wood, T.G., 1968. Preliminary studies of the role of *Nasutitermes exitiosus* (Hill) in the cycling of organic matter in a yellow podzolic soil under dry sclerophyll forest in South Australia. *Trans. 9th Int. Congr. Soil Sci. Adelaide, S.A.*, 2: 11–18.

Levieux, J., 1969. L'échantillonnage des peuplements de fourmis terricoles. In: M. Lamotte and F. Bourlière (Editors), *Problèmes d'écologie: L'échantillonnage des peuplements animaux des milieux terrestres.* Masson, Paris, pp. 289–300.

Lions, J.C., 1966. Contribution à l'étude écologique des Oribates (Acariens) du sol dans la chaîne de la Trévaresse (B.-d.-Rh.). *Rev. Ecol. Biol. Sol*, 3: 495–510.

Lions, J.C., 1975. Application du concept de la diversité spécifique à la dynamique de trois populations d'Oribates (Acariens) de la forêt de la Sainte Baume (Var). 1ère partie: Résultats généraux et variabilité temporelle globale. *Ecol. Mediterr.*, 1: 165–192.

Lions, J.C., 1977. Application du concept de la diversité spécifique à la dynamique de trois populations d'Oribates (Acariens) de la forêt de la Sainte Baume (Var). 2ème partie: Variabilité temporelle selon les différents niveaux prospectés. *Ecol. Mediterr.*, 3: 85–104.

Lloyd, M. and Ghelardi, R.J., 1964. A table for calculating the "equitability" component of species diversity. *J. Anim. Ecol.*, 33: 217–225.

Löffler, H., 1966. Beitrag zur Kenntnis der Harpacticiden- und Ostracodenfauna Chiles. *Zool. Anz.*, 176: 192–205.

Loots, G.C. and Ryke, P.A.J., 1966. A comparative quantitative study of the microarthropods in different types of pasture soil. *Zool. Afr.*, 1: 167–192.

Loots, G.C. and Ryke, P.A.J., 1967. The ratio Oribatei:Trombidiformes with reference to organic matter content in soils. *Pedobiologia*, 7: 121–124.

Lossaint, P. and Rapp, M., 1978. La forêt méditerranéenne de chênes verts (*Quercus ilex* L.). In: M. Lamotte and F. Bourlière (Editors), *Problèmes d'écologie: Structure et fonctionnement des écosystèmes terrestres.* Masson, Paris, pp. 129–185.

Loub, W., 1963. Untersuchungen zur Mikrobiologie afrikanischer Böden. *Bodenkultur*, 14: 189–208.

Mahunka, S., 1968. The scientific results of the Hungarian soil zoological expedition to South America. 4 Acari: Scutacaridae 1. A survey of the scutacarid fauna of Chile. *Acta Zool. Hung.*, 14: 139–166.

Marcuzzi, G., 1951. I Tenebrionidi come indicatori del clima. *Riv. Biol.*, 43: 399–437.

Marcuzzi, G., 1964. Prima applicazione della teoria

dell'informazione allo studio dell'ecologia animale nell'ambiente edafico. *Riv. Biol.*, 57: 35–53.

Marcuzzi, G., 1966. Preliminary quantitative observations on the soil fauna near Padova (Colli Euganei). *Pedobiologia*, 6: 219–225.

Marcuzzi, G., 1968. Osservazioni ecologiche sulla fauna del suolo di alcune regioni forestali italiane. *Ann. Centro Econ. Montana Venezie*, 8: 209–331.

Marcuzzi, G. and Dalla Venezia, L., 1972. First results of the study of the soil fauna of two Italian artificial ecosystems. *Rev. Ecol. Biol. Sol*, 9: 229–233.

Marcuzzi, G. and Di Castri, F., 1967. Osservazioni ecologico-quantitative sulla fauna del suolo di Recoaro (Prealpi Venete). *Mem. Mus. Civ. Stor. Nat., Verona*, 15: 159–172.

Marcuzzi, G., Lorenzoni, A.-M. and Di Castri, F., 1970. La fauna del suolo di una regione delle Prealpi Venete (M. Spitz, Recoaro). Aspetti autoecologici. *Atti Ist. Veneto Sci., Lett. Arti*, 128: 411–567.

Margalef, R., 1957. La teoria de la información en ecologia. *Mem Real Acad. Cienc. Art. Barcelona*, 32: 373–449.

Martínez, T. and Sánchez, M., 1962. *Observaciones ecológico-cuantitativas sobre la fauna edáfica de terrenos regados.* Thesis, Universidad de Chile, Santiago, 36 pp.

Matte, V., 1971. *Pinus radiata* plantations in Chile: present situation and future possibilities. In: P. Duvigneaud (Editor), *Productivity of Forest Ecosystems. Proceedings of the Brussels Symposium.* Ecology and Conservation 4. UNESCO, Paris, pp. 217–223.

Medina, P., 1967. Estudio microbiológico de la serie de suelos Lo Vásquez, bajo dos condiciones de manejo. *Agric. Téc.*, 27: 75–82.

Menke, J.W. and Villaseñor, R., 1977. The California mediterranean ecosystem and its management. In: H.A. Mooney and C.E. Conrad (Editors), *Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems.* Forest Service, U.S. Department of Agriculture, Washington, D.C., pp. 257–270.

Merny, G. and Luc, M., 1969. Les techniques d'échantillonnage des peuplements de nématodes dans le sol. In: M. Lamotte and F. Bourlière (Editors), *Problèmes d'écologie: L'échantillonnage des peuplements animaux des milieux terrestres.* Masson, Paris, pp. 237–272.

Montero, A. and Christen, E., 1974. *Meso y macro fauna edáfica en terrenos naturales e intervenidos de la región del Maule.* Publicación regional No. 4, Universidad de Chile, Talca, 53 pp.

Mooney, H.A. (Editor), 1977. *Convergent Evolution in Chile and California, Mediterranean Climate Ecosystems.* Dowden, Hutchinson and Ross, Stroudsburg, Penn., 224 pp.

Motta, S. and Petralia, A., 1973. Osservazioni sulla biologia di due specie di Acari Oribatei del suolo della lecceta di M. Minardo. *Boll. Sedute Accad. Gioenia Sci. Nat. Catania*, 12: 341–358.

Murúa, R., 1966. *Estudio ecológico-cuantitativo de la fauna hipogea de las dunas Concon-Quintero.* Thesis, Universidad de Chile, Santiago, 47 pp.

Najt, J. and Rubio, I., 1978. Tullbergiinae sud-américaines. I. Le genre *Dinaphorura* (Coll.). *Nouv. Rev. Entomol.*, 8: 95–112.

Noodt, W., 1961. Über Tierarmut in Chile. *Ver. Dtsch. Zool. Ges. Saarbrücken*, 1961: 433–437.

Noodt, W., Sáiz, F. and Juhl-Noodt, H., 1962. Corte ecológico transversal de Chile Central con consideración de los Artrópodos terrestres. *Invest. Zool. Chil.*, 8: 65–117.

Olivier, P.G. and Ryke, P.A.J., 1965. Seasonal fluctuations of the mesofauna in soil under kikuyu grass. *Mem. Inst. Invest. Cient. Moçambique*, 7: 235–279.

ONU–MINAGRI (Organización Naciones Unidas – Ministerio de Agricultura), 1970. *Estudios sobre actividad de las poblaciones microbianas en suelos chilenos.* Proyecto de estudios y reconocimiento de suelos chilenos. Ministerio de Agricultura de Chile, Santiago, 95 pp.

Parkinson, D., Gray, T.R.G. and Williams, S.T., 1971. *Methods for Studying the Ecology of Soil Microorganisms.* IBP Handbook No. 19. Blackwell, Oxford. 128 pp.

Phillipson, J. (Editor), 1971. *Methods of Study in Quantitative Soil Ecology: Population, Production and Energy Flow.* IBP Handbook No. 18. Blackwell, Oxford, 297 pp.

Pianka, E.R., 1970. On *r*- and *K*-selection. *Am. Nat.*, 104: 592–597.

Pochon, J., De Barjac, H. and Faivre-Amiot, 1959. L'influence de plantations d'*Eucalyptus* au Maroc sur la microflore et l'humus du sol. *Ann. Inst. Pasteur*, 97: 403–406.

Poinsot-Balaguer, N., 1971. Ethologie de quelques espèces de Collemboles Isotomides de Provence. *Ann. Univ. Prov.*, 45: 33–53.

Poinsot-Balaguer, N., 1974. Comportement de certains Collemboles dans les biotopes xériques méditerranéens: un nouveau cas d'anhydrobiose. *C.R. Acad. Sci. Paris*, 278: 2213–2215.

Poinsot-Balaguer, N., 1975a. Influence d'une irradiation gamma chronique sur la microfaune d'un écosystème méditerranéen à Cadarache. In: J. Vaněk (Editor), *Progress in Soil Zoology. Proceedings of the 5th International Colloquium on Soil Zoology held in Prague, September 1973.* W. Junk, The Hague, and Academia, Prague, pp. 241–247.

Poinsot-Balaguer, N., 1975b. Influence des facteurs abiotiques sur la dynamique des peuplements de Collemboles de la sansouire camarguaise. *Ecol. Mediterr.*, 1: 193–201.

Poinsot-Balaguer, N., 1976a. Dynamique des communautés de Collemboles en milieu xérique méditerranéen. *Pedobiologia*, 16: 1–17.

Poinsot-Balaguer, N., 1976b. Réponse des communautés de Collemboles à l'irradiation gamma chronique d'une forêt méditerranéenne. *Rev. Ecol. Biol. Sol*, 13: 365–380.

Quintanilla, V.G., 1977. La evolución regresiva de la vegetación en la cuenca de Quillota, curso medio del rio Aconcagua. *Inform. Geogr., Univ. Chile*, No. 24: 17–32.

Ramazzotti, G., 1962a. Il Phylum Tardigrada. *Mem. Ist. Ital. Idrobiol.*, 14: 1–595.

Ramazzotti, G., 1962b. Tardigradi del Cile, con descrizione di quattro nuove specie e di una nuova varietà. *Atti Soc. Ital. Sci. Nat. Mus. Civ. Storia Nat. Milano*, 101: 275–287.

Ramazzotti, G., 1964a. Tardigradi del Cile — II — con descrizione di due nuove specie e note sulla scultura degli Echiniscidae. *Atti Soc. Ital. Sci. Nat. Mus. Civ. Storia Nat. Milano*, 103: 89–100.

Ramazzotti, G., 1964b. Tardigradi del Cile — III — con

descrizione delle nuove specie *Oreella minor* e *Pseudechiniscus lateromamillatus*. *Atti Soc. Ital. Sci. Nat. Mus. Civ. Storia Nat. Milano*, 103: 347–355.

Ramazzotti, G., 1965. Il Phylum Tardigrada (1° Supplemento). *Mem. Ist. Ital. Idrobiol.*, 19: 101–212.

Ranzoni, F.V., 1968. Fungi isolated in culture from soils of the Sonoran Desert. *Mycologia*, 60: 356–371.

Rapoport, E.H. and Rubio, I., 1963. Fauna Colembológica de Chile. *Invest. Zool. Chil.*, 9: 95–124.

Rapoport, E.H. and Rubio, I., 1968. Fauna Colembológica de Chile II. *Acta Biol. Ven.*, 6: 52–67.

Raven, P.H., 1973. The evolution of mediterranean floras. In: F. di Castri and H.A. Mooney (Editors), *Mediterranean Type Ecosystems, Origin and Structure*. Ecological Studies, Analysis and Studies, 7. Springer-Verlag, Berlin, pp. 213–224.

Robaux, P., 1969. Quelques données biogéographiques sur la répartition des Thrombidiidae. In: *Proceedings of the 2nd International Congress of Acarology, 1967*. Akadémiai Kiadó, Budapest, pp. 67–72.

Rubio, I., 1974. Fauna Colembológica de la Peninsula Muñoz Gamero (Provincia de Magallanes, Chile). *Physis*, 33: 125–131.

Rubio, I. and Hermosilla, W., 1971. Estudios ecológicos en el Archipiélago de Juan Fernández: I. — Biocenosis edáficas en la cumbre del Cerro Alto (Isla Masatierra). *Bol. Mus. Nac. Hist. Nat. Chile*, 32: 41–48.

Rundel, P.W. and Weisser, P.J., 1975. La Campana, a new national park in central Chile. *Biol. Conserv.*, 8: 35–46.

Sáiz, F., 1963a. Estudios synecológicos sobre Artrópodos terrestres en el bosque de "Fray Jorge". *Invest. Zool. Chil.*, 9: 151–162.

Sáiz, F., 1963b. Observaciones synecológicas sobre Artrópodos terrestres en el bosque relicto de Zapallar. *Invest. Zool. Chil.*, 10: 9–25.

Sáiz, F., 1969. *Nothoesthetus*, nouveau genre humicole et endogé des *Euaesthetinae* chiliens (Col. Staphylinidae). *Bull. Soc. Hist. Nat. Toulouse*, 105: 295–310.

Sáiz, F., 1973. Biogeography of soil beetles in mediterranean regions. In: F. di Castri and H.A. Mooney (Editors), *Mediterranean Type Ecosystems, Origin and Structure*. Ecological Studies, Analysis and Synthesis, 7. Springer-Verlag, Berlin, pp. 285–294.

Sáiz, F., 1977. Soil beetles. In: N.J.W. Thrower and D.E. Bradbury (Editors), *Chile-California Mediterranean Scrub Atlas. A Comparative Analysis*. Dowden, Hutchinson and Ross, Stroudsburg, Penn., pp. 184–194.

Sáiz, F. and Di Castri, F., 1971. La fauna de terrenos naturales e intervenidos en la región valdiviana de Chile. *Bol. Mus. Nac. Hist. Nat. Chile*, 32: 5–16.

Sasson, A., 1967. Recherches écophysiologiques sur la flore bactérienne de sols de régions arides du Maroc. *Trav. Inst. Sci. Chérifien Fac. Sci., Ser. Bot. Biol. Vég.*, No. 30: 5–231.

Sasson, A. and Daste, P., 1963. Observations nouvelles concernant l'écologie de l'*Azotobacter* dans certains sols arides du Maroc. *C.R. Acad. Sci. Paris*, 257: 3516.

Schaefer, R., 1973. Microbial activity under seasonal conditions of drought in mediterranean climates. In: F. di Castri and H.A. Mooney (Editors), *Mediterranean Type Ecosystems, Origin and Structure*. Ecological Studies. Analysis and Synthesis, 7. Springer-Verlag, Berlin, pp. 191–198.

Scheller, U., 1968. Chilean and Argentinian Pauropoda. In: C. Delamare Deboutteville and E. Rapoport (Editors), *Biologie de l'Amérique Australe, 4*. Centre National de la Recherche Scientifique (C.N.R.S.), Paris, pp. 275–306.

Schlegel, F., 1962. Hallazgo de un bosque de cipreses cordilleranos en la provincia de Aconcagua. *Bol. Univ. Chile*, No. 32: 43–46.

Schlegel, F., 1966. Pflanzensoziologische und floristische Untersuchungen über Hartlaubgehölze im La Plata-Tal bei Santiago de Chile. *Oberhess. Ges. Nat. Heilkd. Giessen*, 34: 183–204.

Sokal, R.R. and Michener, C.D., 1958. A statistical method for evaluating systematic relationships. *Univ. Kansas Sci. Bull.*, 38: 1409–1438.

Sokal, R.R. and Sneath, P.H.A., 1963. *The Principles of Numerical Taxonomy*. W.H. Freeman, San Francisco, Calif., 359 pp.

Sørensen, T., 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analysis of the vegetation on Danish commons. *Vidensk. Selsk. Biol. Skr.*, 5: 1–34.

Specht, R.L., 1979. Heathlands and related shrublands of the world. In: R.L. Specht (Editor), *Heathlands and Related Shrublands, A. Descriptive Studies*. Ecosystems of the World, 9. Elsevier, Amsterdam, pp. 1–18.

Specht, R.L., 1980. Evolution of the Australian flora: some generalizations. In: A. Keast (Editor), *Ecological Biogeography of Australia*. W. Junk, The Hague, in press.

Travé, J., 1963. Écologie et biologie des Oribates (Acariens) saxicoles et arboricoles. *Vie Milieu, Suppl.*, 14: 1–267.

Turnbull, J.W. and Pryor, L.D., 1978. Choice of species and seed sources. In: W.E. Hillis and A.G. Brown (Editors), *Eucalypts for Wood Production*. CSIRO and Griffin Press Limited, Adelaide, S.A., pp. 6–65.

Van den Berg, R.A. and Ryke, P.A.J., 1968. A systematic–ecological investigation of the acarofauna of the forest floor in Magoebaskloof (South Africa) with special reference to the Mesostigmata. *Rev. Biol.*, 6: 157–234.

Van der Drift, J., 1951. Analysis of the animal community in a beech forest floor. *Tijdschr. Entomol.*, 94: 1–168.

Vannier, G. 1970. *Réactions des Microarthropodes aux variations de l'état hydrique du sol. Techniques relatives à l'extraction des Arthropodes du sol*. Editions du Centre National de la Recherche Scientifique (C.N.R.S.), Paris, 319 pp.

Vannier, G., 1973. Originalité des conditions de vie dans le sol due à la présence de l'eau: importance thermodynamique et biologique de la porosphère. *Ann. Soc. R. Zool. Belg.* 103: 157–167.

Vannier, G. and Cancela da Fonseca, J.-P., 1966. L'échantillonnage de la microfaune du sol. *Terre Vie*, 1: 77–103.

Vitali-di Castri, V., 1962. La familia Cheiridiidae (Pseudoscorpionida) en Chile. *Invest. Zool. Chil.*, 8: 119–142.

Vitali-di Castri, V., 1963. La familia Vachoniidae (= Gymnobisiidae) en Chile (Arachnidea, Pseudoscorpionida). *Invest. Zool. Chil.*, 10: 27–82.

Vitali-di Castri, V., 1966. Observaciones biogeográficas y filogenéticas sobre la familia Cheiridiidae (Pseudoscorpionida). In: *Progresos en Biologia del Suelo. Actas del Primer Coloquio Latinoamericano de Biologia del Suelo*. Monografias I, UNESCO, Montevideo, pp. 379–386.

Vitali-di Castri, V., 1969a. Tercera nota sobre los Cheiridiidae de Chile (Pseudoscorpionida) con descripción de *Apocheiridium (Chiliocheiridum) serenense* n. subgen., n.sp. *Bol. Soc. Biol. Concepción*, 41: 265–280.

Vitali-di Castri, V., 1969b. Revisión de la sistemática y distribución de los *Gymnobisiinae* (Pseudoscorpionida, Vachoniidae). *Bol. Soc. Biol. Concepción*, 42: 123–135.

Vitali-di Castri, V., 1969c. Remarques sur la famille des Menthidae (Arachnida, Pseudoscorpionida) à propos de la présence au Chili d'une nouvelle espèce, *Oligomenthus chilensis. Bull. Mus. Nat. Hist. Nat. Paris*, 41: 498–506.

Vitali-di Castri, V., 1972. El género sudamericano *Gigantochernes* (Pseudoscorpionida, Chernetidae) con descripción de dos nuevas especies. *Physis*, 31: 23–38.

Vitali-di Castri, V., 1973. Biogeography of Pseudoscorpions in the mediterranean regions of the world. In: F. di Castri and H.A. Mooney (Editors), *Mediterranean Type Ecosystems, Origin and Structure*. Ecological Studies, Analysis and Synthesis, 7. Springer-Verlag, Berlin, pp. 295–305.

Vitali-di Castri, V., 1975. Deux nouveaux genres de Chthoniidae du Chili: *Chiliochthonius* et *Francochthonius* (Arachnida, Pseudoscorpionida). *Bull. Mus. Natl. Hist. Nat., Paris, 3e Sér.*, No. 334: 1277–1291.

Vitali-di Castri, V. and Di Castri, F., 1970. L'évolution du dimorphisme sexuel dans une lignée de Pseudoscorpions. *Bull. Mus. Natl. Hist. Nat., Paris*, 42: 382–391.

Wallwork, J.A., 1972. Distribution patterns and population dynamics of the microarthropods of a desert soil in southern California. *J. Anim. Ecol.*, 41: 291–310.

Wallwork, J.A., 1976. *The Distribution and Diversity of Soil Fauna*. Academic Press, London, 355 pp.

Warburg, M.R., 1965. Water relations and internal body temperature of isopods from mesic and xeric habitats. *Physiol. Zool.*, 38: 99–109.

Warburg, M.R., 1968. Behavioural adaptations of terrestrial isopods. *Am. Zool.*, 8: 545–559.

Wood, T.G., 1970. Micro-arthropods from soils of the arid zone in Southern Australia. *Search*, 1: 75.

Wood, T.G., 1971. The distribution and abundance of *Folsomides deserticola* Wood (Collembola, Isotomidae) and other microarthropods in arid and semi-arid soils in southern Australia, with a note on nematode populations. *Pedobiologia*, 11: 446–468.

Yeilding, L. 1977. Decomposition in chaparral. In: H.A. Mooney and C.E. Conrad (Editors), *Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems*. Forest Service, U.S. Department of Agriculture, Washington, D.C., pp. 419–425.

Young, A. 1979. Mapping the world's soils. *New Sci.*, January 1979: 252–254.

Zeiss, E., 1967. *Estudio ecológico-cuantitativo de la fauna hipogea en la isla Masatierra (Archipiélago Juan Fernández)*. Thesis, Universidad de Chile, Santiago, 48 pp.

Zinke, P.J., 1973. Analogies between the soil and vegetation types of Italy, Greece, and California. In: F. di Castri and H.A. Mooney (Editors), *Mediterranean Type Ecosystems, Origin and Structure*. Ecological Studies, Analysis and Synthesis, 7. Springer-Verlag, Berlin, pp. 61–80.